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MIGRATION AS A FACTOR IN EVOLUTION: ITS ECOLOGICAL DYNAMICS[1]

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I. INTRODUCTION

MY subject, "Migration as a Factor in Evolution," is, in other words, the function or rôle of migration in evo-

[1] This paper was prepared, by invitation, for the symposium on the Factors of Evolution, at the Pittsburgh meeting of the American Society of Naturalists and an abstract of this paper, entitled "Migration as a Factor in Evolution," was read January 1, 1918. Dr. G. H. Shull, president of the society, has kindly consented to its publication in advance of the volume which is to contain all the papers of the symposium.

lution.[2] In view of the recent concentration of interest on heredity, my subject has the flavor of an old-fashioned one, which calls back to the days when Darwin and Wallace were living, and when Wallace's "Island Life" was frequently read with enthusiasm, and when there was possibly a more general belief that natural selection was one of the large factors in evolution. But progress has not been limited to the studies of heredity, for with the rapid rise of certain phases of general physiology, animal behavior and animal ecology, a newer orientation is now possible with regard to the migration of animals by both the active and passive methods. For our knowledge of animal responses, as well as the influence of the vegetational and physical environment, have made considerable progress, and we now probably see more clearly than ever before the intimate relation existing between the animals and the conditions which influence their migrations. The present occasion has thus furnished an opportunity to make a preliminary reorganization of the accumulated materials from a somewhat different standpoint than was formerly current in discussing migration. And although some of these ideas are widespread and even commonplace in certain limited fields, yet they are not yet in as general use as is desirable, and they are in urgent need of extended application and critical study.

In the following discussion of migration as an evolutionary factor, I wish to emphasize two points in particular. One is the discussion of the process of analysis and the other is to suggest some methods of applying this method to the problem of migration. It may seem aside from the main thesis to give this emphasis to the process method of evolution, but after striving several years for the conscious application of this method in an allied field (Adams '13, '15), and seeing its beneficial results there,

[2] By evolution, I mean to use the term in the broadest possible sense—to include all changes within the organism and its necessary environmental implications, and not as limited to the "species problem." This term must be as thoroughgoing as metabolism in physiology, or as metamorphism as applied to rocks by Van Hise, "any change in the constitution of any kind of rock."

and furthermore, not having seen this formulated and applied to evolution as here presented, I feel that the importance of the subject merits this treatment.

Special attention is called to the fact that this discussion is not intended as a complete, scientific explanation of migrational facts, but as the presentation of a point of view, or working hypothesis, which it is believed will aid in explaining many well-known facts and relations, and will aid in the discovery of new ones. An effort has been made to frame this hypothesis in such a manner as not to prejudice the problems investigated, or to interfere seriously with the various constructive schools of investigation, although I am well aware that this hypothesis, like all others, is built upon certain assumptions.

During the preparation of this paper (which amplifies certain ideas which I have previously outlined) I was much impressed by finding so much confirmatory evidence of the general validity of the dynamic standpoint, in fields relatively remote from migration. The independent growth of such conceptions in diverse fields is indicative that many subjects are independently reaching a certain common stage of development and that spontaneously such ideas are becoming independent organizing centers of activity. By interaction and regulation among these ideas, new higher systems of unity and correlation are developing, which are producing important effects in zoology as well as in other sciences. The slowness seen in the application of dynamic ideas to biology is perhaps rather natural as is evident when we recall the fact that even in the simpler physical sciences we have as yet no complete dynamical theory or system, although much progress has been made, not, however, toward a complete system, but toward that dynamic equilibrium which characterizes a growing subject.

II. The Process Method of Animal Responses

1. Introduction

The fundamental assumption upon which this discussion is founded is that the animal should be looked upon

as an entity or agent whose system of activity or responses to internal and external influences are its most fundamental characteristic. The activity of the animal, as an agent, is its *process* of change or its process of activity. Broadly speaking, this is a study of influences, of response or behavior, a study of what animals do and how they do it. Throughout it is the *dynamic* aspect of the animal; the pressure it exerts upon the environment; and the pressure exerted by the environment on it, that is of greatest importance. I see no reason why these assumptions can not be of universal application, and why they can not be accepted in all investigation. This view appears to be so well established that no detailed evidence and discussion of it seems necessary at this time. The animal agent itself is not a fixed thing, but one which runs through a cycle; it originates, develops and disintegrates and is thus in its maintenance subject to all the ebb and flow of other processes, and has similar dynamic relations. There is thus valid reason for assuming a thoroughgoing process or dynamic program for dealing with all animal problems. The same is equally true of all plants which form a part of the animal environment, and the physical environment lends itself, in fact, easily leads, in such a treatment, and fits into this scheme harmoniously, and makes it possible to give not only a uniform treatment to all phases of animal relations, but enables the student of animals to make a perfect contact with all the allied sciences, and to draw from each one all possible support, with the least possible friction and interference.

2. Dynamic Principles

(*a*) *Activity of Agent.*—In discussing animal problems from the process standpoint there are several conceptions which are fundamental. These ideas can be illustrated in simple form by an example from physical science. Running water is a substance combined with energy (gravitation) which exerts stress or pressure, which it expends upon other substances, and it is therefore an agent. An agent thus exerting stress and expend-

ing gravitational energy upon other substances is in the process of activity. Thus, running water, by the general process of erosion, including the subsidiary processes of weathering and transportation, wears down the land and results in the formation of many features such as brooks, creeks, plains, deltas, and a variety of other physiographic products. An organism is also an agent which expends physical and chemical energy, producing stress and exerting pressure and expending energy on other substances, exhibits its process of response or its *process of behavior.* An animal, by the process of predation runs down another animal and devours it, by its *process* of digestion dissolves it, and by the process of assimilation makes muscle, bone, feathers or fur out of it, and these are all products of its activity. The process of response is here strictly comparable to the process of erosion of running water, and their products are similarly comparable. The general process is generic and includes many species and varieties of subsidiary processes, *ad infinitum.* As Keyes ('98) has well said, "Processes are merely operative. If coupled with products at all . . . they must be regarded as formative or constructive. The product's destruction, its loss of identity, is wholly immaterial. The action of agencies is merely to produce constant change." It is, therefore, to the process of living, to the process of evolution, rather than to its products such as species, varieties, etc., which are of fundamental importance. For this reason the products must be subordinated to the agencies and processes, because the laws of change are in reality the object sought.

The physiographer is not content to rest with the idea that the agent, as, for example, running water, is the finished product of his analysis, for he also applies the same methods of investigation to the agent itself, in order to know its method of origin, the *process* by which it originates in the stream, whether indirectly from a spring, or directly from the clouds. Thus the same methods which the physiographer uses in studying the activity of the agent, he again uses to explain the origin or derivation

of the agent iself. The investigator of animals follows the same plan. He likewise uses the same kind of methods in the investigation of the processes of functional and structural development, not only as applied to the actions of the agent, but to its origin as well, and thus again we are justified in concluding that the process method is of universal application.

(*b*) *Cycle of Activity.*—The activity of agents is always accompanied by the expenditure of energy. This expenditure does not take place at a uniform rate, there is a pulsation, an ebb and flow, a rising and a falling. Periods of activity are followed by periods of repose and a rhythm is seen which can often be resolved into cycles. The importance of determining such cycles has been well expressed by Lockyer[3] as follows:

> Surely in meteorology, as in astronomy, the thing to hunt down is a cycle, and if that is not to be found in the temperate zone, then go to the frigid zones, or the torrid zones and look for it, and if found, then above all things, and in whatever manner, lay hold of, study it, record it, and see what it means. If there is no cycle, then despair for a time if you will, but yet plant firmly your science on a physical basis . . . and having gotten such a basis as this, wait for results.

There are innumerable cycles in the responses of animals, and of these the life-history cycle is perhaps the most generally recognized; but activity and response, hunger and satiety, stimulation and response, are other familiar expressions of these conditions. During these cycles of change the relative amount of energy set free varies greatly, in other words, its *dynamic status* changes. As expressed elsewhere, I have stated ('15, p. 10):

> When a great amount of energy is being set free, when an animal is exerting much influence, we may look upon it as producing pressure or strain. A condition of stress is not a permanent one, because the pressure tends to cause such changes as will equalize or relieve this condition. This is considered as the process of adjustment to strain, and is Bancroft's law ('11). An animal in an unfavorable condition is stimulated, its normal activities are interfered with, and a physiological condition of stress is produced which lasts until, by repeated responses or

[3] "Solar Physics," 1874, pp. 424–425.

"trials," the animal escapes stimulation or succumbs and a relative equilibrium is established. An area becomes overpopulated and consequently there may be established a condition of stress which results in an adjustment by a reduction (through many causes) in the excess of population and a restoration of the normal, or a condition of relative equilibrium. From these examples it may be seen that the *dynamic status* means the condition of a unit or system with regard to its degree of relative equilibrium. The cycle of change may be considered to begin at any point. I have taken as the initial stage of the cycle the condition of *stress* and *pressure* and have indicated how this condition tends to change in response to pressure, bringing about the *process* of adjustment to strain, and leading to the *condition* of adjustment to strain, or that of relative equilibrium. The activity of the agent produces the condition of stress, the process of adjustment to the strain follows, and this leads to the product—the establishment of the condition of adjustment or of relative equilibrium.

These ideas can be well applied to the life cycle, as is indicated from the following statement by Sedgwick ('10, p. 177), who says:

> The life-cycle, of which the embryonic and larval periods are a part, consists of the orderly interaction between the organism and its environment. The action of environment produces certain morphological changes in its organism. These changes enable the organism to come into relation with new external forces, to move into what is practically a new environment, which in its turn produces further structural changes in the organism. These in turn enable, indeed necessitate, the organism to move again into a new environment, and so the process continues until the structural changes are of such a nature that the organism is unable to adapt itself to the environment in which it finds itself. The essential condition of success in this process is that the organism should always shift into the environment to which the new structure is suited—any failure in this leading to impairment of the organism. In most cases the shifting of the environment is a very gradual process (whether consisting in the very slight and gradual alteration in the relation of the embryo as a whole to the egg-shell or uterine wall, or in the relations of its parts to each other, or in the successive phases of adult life), and the morphological changes in connection with each step of it are but slight. But in some cases jumps are made such as we find in the phenomena known as hatching, birth, and metamorphosis. . . . And with this property of reacting to the environment goes the further property of undergoing a change which alters the relation of the organism to the old environment and places it in a new environment.

It is seldom indeed that one finds ontogeny so clearly expressed in terms of an active agent which is under-

going a cycle of changes—both in structure and function—and is being stimulated, responding, behaving, and even migrating into new environments, in response to internal and external stimulation. This is indicative of the dawn of a new era in the study of ontology (cf. Thompson, '17). As Bancroft ('11, p. 178) suggested, Sedgwick ('10, p. 177) saw clearly for the moment, as it were, but not in practice and concretely, the dynamic conception of individual development, although it is very evident that he saw the unity or continuity of the ontogenetic cycle. However, it has remained for Child ('15, '15*a*, '15*b*) who, apparently adapting largely the dynamic conceptions of the plant and animal ecologists, and to a lesser degree those of the physiologists, has now given expression, in a clear and concrete manner, to the dynamic ideas in individual developmental responses, and special attention is called to his important work.

That the life cycle varies in its degree of susceptibility to environmental influence has been pointed out by Vernon ('99, p. 199), DeVries (1900), Bancroft ('11, p. 175), and others (Woods, '10; Pike and Scott, '15; Pike, '17). Vernon's law is expressed ('03, p. 199) as follows: "In fact, it would seem to be a law of general application that *the permanent effect of environment on the growth of a developing organism diminishes rapidly and regularly from the time of impregnation onwards.*" Bancroft was the first to see that his law included Vernon's. He said ('11, p. 175):

> We know that, as we get older, our tendency to resist change increases; our habits of body and mind become more fixed.[4] We should therefore be tempted to conclude that the resistance to change increases as the organism becomes mature and that a given stimulus would probably have the most effect if applied at or before the earliest stages of development.

[4] In this connection it is interesting to recall the influence which this law may have upon scientific research. Once Clerk-Maxwell wrote to Herbert Spencer about some point in his "First Principles" as follows: "It is seldom that any man who tries to form a system can prevent the system from forming around him; and closing him in before he is forty. Hence the wisdom of putting in some ingredient to prevent crystallization and keep the system in a colloidal condition." (Footnote by C. C. A.)

He then quotes Vernon and continues:

> If the pressure on a liquid is made less than the vapor pressure for that liquid at that temperature, some of the liquid vaporizes, the temperature falls, and the liquid may be said to adapt itself to the new conditions. What would happen if the liquid were not adaptable? The easiest way to obtain non-adaptable liquid is to place a Bunsen burner under it. The temperature rises until the boiling point is reached. The liquid then ceases to be adaptable. It volatilizes, it disappears, it becomes extinct so far as that particular region or flask is concerned. If a species can not adapt itself to changed climate or other conditions, it does not volatilize; but it disappears, it becomes extinct. It may be a new point of view to consider the extinction of the mastodon as analogous to the distillation of water; but the two cases are really parallel, except in time.

These facts are of the greatest importance because they indicate the *critical stage or condition* at which, in the migration of animals into new localities and conditions, organisms are most likely to be modified, and thus influence their evolution. This furnishes a new reason for stressing the importance of the breeding conditions and habitat in ecology.

An exception to Vernon's law is to be seen in the case of the Protozoans (and probably to other kinds of non-sexual reproduction), as is indicated by Jennings ('12, '13) and Woodruff's investigations, which show that in a proper environment the inertia of the life cycle tends to continue on indefinitely and does not run down. Jennings ('12, pp. 573–574) shows that conjugation in Protozoa and sexual reproduction in the metazoa cause diverse and new combinations of characters. In other words, this means that the processes of conjugation (favored by adverse conditions) and sexual reproduction, tends to break up the stability and crystallization into which the ontogenetic system tends to develop, and tends to restore, as it were, flexibility and a colloidal state to the race. This changes the system so as to minimize the interference with its processes. In the metazoan the number of systems is so large, that in spite of its chemical integration and regulation, interference with one or more of

them, possibly the "slowest," limits action and causes death. As indicated later, according to the phase rule the greater the number of "phases" interacting the lesser the number of possibilities of change. This is not a condition limited to organisms, but is a general law. It is perhaps in some sense as this that we can concede "differentiation" as a cause of death.

The animal as an agent, or individual, behaves according to its own system, to the extent that it is an independent unit, and these activities are cyclical. All systems tend to perpetuate themselves. Bancroft's law for all systems is that: "The broadest definition of it is that a system tends to change so as to minimize an external disturbance." In other words this is a perpetuating tendency, a method of assimilation, of which reproduction may be considered but a special phase; it is not solely a peculiarity of organisms, as is often stated, but of *all systems*. Sedgwick ('10, p. 177) has said: "It is a property of living matter to react in a remarkable way to external forces without undergoing destruction. . . . This property of reacting to the environment without undergoing destruction is, as has been stated, a fundamental property of organisms." In these features the animal acts only as other systems tend; as a catalyzer, it hastens changes and maintains itself. The activity of the animal, its centrifugal stress, causes it to collide with its environment, while, on the other hand, there is the environmental bombardment, both of which, within certain limits, tend to interfere or destroy the animal. On the other hand, the tendency of the system is to "minimize disturbance," to change within, to minimize, to "retreat" from interference (absolutely or relatively), and in this manner to a large degree, the system is perpetuated. To be sure, many individuals perish, but the system of the species continues. The rate of change of the system can be modified only as fast as its *slowest member* can change, and on this account many individual systems are destroyed.

In addition to influences which "interfere" with sys-

tems, as expressed by Bancroft, there are those which *reinforce* or accelerate (tend to continue or hasten activity) and do not change its character, but only the intensity of the response (temperature, enzymes, repetition, etc.). By this method also systems tend to be perpetuated, and organisms in "favorable" (non-interfering) conditions, tend to continue their normal activities.[5] This law appears to be a corollary of Bancroft's law which is concerned with interference or retardation. Thus when a system is *reinforced,* rather than disturbed, the system continues onward in its normal cycle without interference, and may even be accelerated in its activities. This is a condition which may maintain a relative equilibrium, or increase stress. The intensity of interference, or reinforcement, and its repetition, hastens or retards the rate of change of a system. We thus have the qualitative and quantitative relations applying to the law of reinforcement or acceleration of the equilibrium, and Bancroft's law of interference with its development.

Even relatively fixed and automatic responses of behavior may be looked upon much as the relatively stable structural characters, so that every sort of behavior, even to the process of higher learning, shows this regulatory influence which tends to change in such a manner as to eliminate all disturbance with its systems, even to the inconsistencies of our ideals.

Thorndike ('11, p. 244) in summarizing the laws of "acquired behavior or learning" formulates two laws. The first is essentially a statement of Bancroft's law of response to interference (discomfort or satisfaction), and the second (exercise or repetition), is that of reinforcement. This means that the kind and intensity of stimulation, and its repetition are the laws of establishing associations, or of changing the system, and that *intensity and repetition* act as the catalyzers which influence the speed of modification of the system; at bottom it therefore appears we have qualitative and a quantitative

[5] Cf. Jennings, '06, p. 295, "positive reactions."

expression of them. Limiting factors, because of their intensity and repetition, tend to change the animal system so as to minimize the external disturbance, or the animal system tends to change in such a manner as to minimize external disturbance, at a speed determined by the intensity and repetition of the disturbance. The so-called "trial and error," or, better, trial method of behavior, is also an independent formulation of Bancroft's law. It seems probable that the modifiability of behavior, and even *all methods of animal regulation, are expressions of these laws of interaction.*

The "balance of nature" is a culminating phase of the cycle of adjustment to strain. As expressed elsewhere, I have said (Adams, '15, p. 14): "When a balanced condition, or relative equilibrium, in nature is referred to, we must not assume that all balances are alike, for some are disturbed with little effort and others are exceedingly difficult to change. This distinction is an important one. Once the balance is disturbed, the process of readjustment begins. This is a phase in the balancing of a complex of forces. Just what stages this process will pass through will depend, to an important degree, upon the extent of the disturbance. Slight disturbances are taking place all the time and grade imperceptibly into the normal process of maintenance, as when a tree dies in the forest and its neighbors or suppressed trees expand and take possession of the vacancy thus formed. Disturbances of a greater degree, on the other hand, may only be adjusted by a long cumulative process. This change can progress no faster than the rate at which its slowest member can advance. Thus a forest association of animals may be destroyed by a fire so severe that all the litter and humus of the forest floor is burned. The animals which live in the moist humic layer as a habitat, such as many land snails, diplopods, and certain insects, can not maintain themselves upon a mineral soil, rock or clay. As such a forest area becomes reforested, these animals can only find the optimum conditions when the slow proc-

ess of humus formation reaches a certain degree of cumulative development. Under such circumstances this later stage must be preceded by antecedent processes, and the restoration of the balance is long delayed. Some adjustments take place so quickly that little can be learned of the stages through which they pass. There are, however, many slow processes which afford an abundance of time for study; in fact some are too slow to study during a life time. The processes which are moderately slow are often particularly illuminating because all stages are frequently so well preserved that comparison is a very useful method of study; the slowness of a process has a certain resolving power, as it were, recalling the influence of a prism upon a beam of white light, which reveals many characteristics obscure to direct vision. A study of the processes of adjustment among animals is a study of an important phase of the problem of maintenance. The continued process of response will, if circumstances permit, lead to a condition of relative adjustment, or balancing among all the factors in operation.'' The determination of the dynamic status and its application to cycles is seen to be a method or criterion which may be used for the determination of cycles of activity, and the repetition of these determinations will indicate the direction of movement of a process, and thus serve as a guide in the determination of its rate of change.

(*c*) *Limiting Factors.*—Animals live in a real world, they are dependent upon an environment and they can not be understood independently of it. They do not live, as it were, in a vacuum. As Brooks ('02, p. 485) has said: ''No physiologist who studies the waste and repair of living bodies, no naturalist who knows living beings in their homes, no embryologist who studies the influence of external conditions upon development, can, for an instant, admit that living beings are self-sufficient or self-sustaining, or that their being is in themselves; for the line we draw, for our study, between living beings and the external world is not one we find in nature, but one

that we make for our own purposes." We have seen that the essence of the animal is its activity. Its life is a continuous collision with the environment and a bombardment by the environment, with changes which tend to relieve the disturbances. This is particularly true of free-living animals, and is indirectly so, even of sedentary and sessile kinds. This radiating activity of the animal, and the direct convergent influence of the environment on the animal, is the basis for the friction and interaction which exists between the organism and the environment. There are, therefore, definite zones of influence and stimulation about the normal or attuned environment of the animal, and with departure from these conditions locally and geographically there are certain definite results (Adams, '04, p. 211):

> The new vital conditions are a cause of stimulation and with further departure (beyond a certain limit) it leads to increased stimulation or to unfavorable conditions. This results in retarded growth, development, and reproduction of the organism as a whole. Thus the end results of extreme departure from the optimum in either direction are similar.

(Adams, '15, pp. 8–9):

> Thus departure from the optimum toward an increase or a decrease, are departures from the most favorable, conditions toward less favorable conditions and hence toward limiting conditions. . . . In nature we look upon the optimum as that complex of habitat factors which is most favorable, and departure in any direction from this optimum intensity is in the direction of a less favorable degree of intensity, or into unfavorable conditions. From this standpoint *any unfavorable condition is a limiting factor* and may retard, hasten, or prevent vital and ecological activities.

(Adams, '13, p. 98):

> The similar results of extremes of high and low . . . temperatures, aridity, and the lack of oxygen may be cited as examples. Such effects have an important bearing upon the subject of physical and chemical *limiting factors* which influence individuals. [Cf. Shelford, '11, pp. 598–599.]

I would now modify my preceding quotations so as to definitely discard the old idea of the optimum,[6] in harmony

[6] This word has a general utility, but its technical value, like that of the "normal," both long considered peculiar to organic response, appears to be limited.

with the suggestions of Blackman and Smith ('11) who show that certain physiological processes are better explained as the "result of interacting limiting factors than by the conception of the optima." This principle is an extension of the law of the minimum and is formulated by them as follows (p. 411):

> The identification of the particular limiting factor in any definite case is carried out by applying experimentally the following general principles. *When the magnitude of a function is limited by one of a set of possible factors, increase of that factor, and of that one alone, will be found to bring about an increase of the magnitude of the function* . . . (p. 397). When several factors are possibly controlling a function, a small increase or decrease of the factor that is limiting, and of that factor only, will bring about an alternation of the magnitude of the functional activity.

Probably this formulation should be broader, and be made to include not only a single factor, but all unfavorable or limiting factors, as I have indicated above, and as both Livingston ('17, p. 8) and as Hooker ('17, p. 201) suggest.

Recent additional physiological evidence of the concentric zonation (gradation) of the limiting factors of temperature and humidity have been made by Pierce ('16). He accepts the older idea of the optimum and thus certain of his results on zonation harmonize with my statement of 1904. He shows that for the cotton boll weevil there is a vertical temperature gradient which influences the metabolism, growth and other activities, and that for a given temperature there is a corresponding horizontal humidity gradient which forms concentric zones of less favorable conditions. These extend from the optimum, through dormancy, on to death. It seems likely, however, that the idea of "interacting limiting factors" explains his facts better than that of the optimum.

The idea of limiting factors in experimental work is now building up a laboratory idea of environmental complexity, even under controlled conditions, which corresponds closely with what the field ecologists have called

an environmental complex. This is a healthy sign as it will greatly assist in the correlation of field and laboratory studies. Recently Livingston ('17, p. 8) has said:

> I wish now simply to emphasize the point that we can no longer speak of a single condition as being a cause of an observed effect. The next generation of physiologists will have to learn to handle more than a single variable and to deal with *complexes* of conditions.[7]

This recalls John Stuart Mill's statement that:

> It is seldom, if ever, between a consequent and a single antecedent that this invariable sequence subsists. It is usually between a consequent and the sum of several antecedents; the concurrence of all of them being requisite to produce, that is, to be certain of being followed by the consequent. In such cases it is very common to single out one only of the antecedents under the denomination of cause, calling the others merely Conditions. . . . The real cause is the whole of these antecedents; and we have, philosophically speaking, no right to give the name of cause to one of them, exclusively of the others. . . . All the conditions are equally indispensable to the production of the consequent; and the statement of the cause is incomplete unless in some shape or other we introduce them all.

When Hooker ('17, p. 201) states that, "It is necessary to get away from the custom of discussing causes, however difficult this may be. The idea of causation invariably indicates *incomplete analysis*," he does not express the full significance of Livingston's remark. We have not yet outgrown Mill's statement.

In addition to its application to the individual animal, Bancroft's law applies with equal force to the dynamic tendencies of plant and animal associations. The dominance of a climax society shows that (Adams, '08, p. 125):

> Such dominance, in general, implies extensive range, relative abundance, and ability to indefinitely succeed or perpetuate itself under given conditions. . . . The primary environmental conditions tend to encroach upon all others. The local conditions thus tend to become transformed in the direction of the dominant environment and to be appropriated by it. The associations . . . are thus given a definite dynamic trend. . . . Minor environments tend to become encroached upon by the dominant regional influences and ultimately to become extinct. The succession of socie-

[7] Cf. Blackman, '05, p. 293, on the limitations of control experiments.

ties of local habitats is a declining one, while that of the geographic or climax habitat is an increasing and ascending one. . . . That the dominant geographic conditions tend to override local influences seems very fairly established because diverse local original conditions are transformed into the climax or dominant type.

To students of human economics (for except ecologists we seem to have almost no students of general economics, including wild animals and plants) Bancroft's law should be a revelation. The interference or friction seen in economics (Conant, '08) should be included under Bancroft's law. That these laws apply to human social conditions as well can easily be tested by any one who will venture to "interfere" with any system of social machinery, whether it be of the family, fashion, church, state or a political party, for very soon the pressure or stress exerted by the "system" will make itself evident, by the processes of coercion, persuasion, ridicule, proselyting, threat, ostracism, or by a final crushing effort; for interference with a dominant system whether it is large or small has but one tendency. Years ago Bagehot ('73, p. 97) clearly recognized what appears to be essentially the laws mentioned above, and applied them with great skill to the development of political history, under the names of "persecution" and "imitation." Persecution corresponding to interference and imitation to acceleration. Hooker ('17, p. 208) not recognizing Bancroft's law, suggests what he calls the "principle of integration" to cover the interaction of the systems which he recognizes. He says: "These systems are invariably overcoming the effects of limiting factors."

(*d*) *Interaction of Systems.*—The next higher category, above the animal system, is the *interaction of the systems,* and their principles of complex action. To be sure, the animal system can not be divorced from its environment, so that several important features of this interrelation have already been discussed briefly. In dealing with the organism and the environment these two gross systems are perhaps the most clearly recognized in biology. The

environmental complexity is so great that it is bewildering to many, particularly to those who have not followed the most recent methods of dealing with the vegetation and gross physical environment. For convenience in handling, this complex may be broken up advantageously into smaller systems or units which are the agencies which influence animals. This plan provides for both their qualitative and quantitative relations, because the agents provide for the qualitative units, and their dynamic relations include their quantitative intensities.

In dealing with the interaction of systems relating to animals, one of the first points to consider is the classification of these systems, and the recognition of the sizes of the units. Many groupings are possible, such as the individual animal, its plant and animal associates, and the numerous factors of the physical environment. Further analytical systems of the vegetational environment can be grouped according to the recognized units current among the students of the genetic aspects of vegetational development (see Cowles, Clements, etc.). For the physical environment the geologists, physiographers and geographers have already made much progress in the analysis of unit systems, which can be used with comparative ease (see Chamberlin, Salisbury, Van Hise, Davis ('09), etc.). In the study of all these systems naturally more progress has been made in their recognition, than in their complex modes of interaction; and the formulation of their laws of interaction is of the greatest importance. There are three models which really come to mind in this connection. These are:

1. The physical model of the interaction of forces, which leads to resultant motion.

2. The application of Bancroft's law to the interaction of all systems.

3. The application of the physical and chemical model of the phase rule of Gibbs to equilibria of all kinds.

These will now be considered in their respective order:

1. The physical model will assist in keeping in mind

the underlying relations that the stresses, exerted by agents, will reinforce, overcome or balance one another, and influence the end result of change. This is a quantitative law. The *inertia* of the process of adjustment, and the *inertia* of equilibria, should be recalled (cf. Newton's first law) in this connection. The conception of inertia appears to have been almost neglected in biology.

2. Bancroft's law, that systems tend to change to minimize external disturbance, is a general law which appears to apply to the *interaction of all systems.* This is a qualitative law, which should be of great practical value.

3. The phase rule, according to Henderson ('13, pp. 257–258) is that the

> condition of equilibrium in any material system depends upon the number of its components, the number of its phases, temperature, pressure, and in general, the concentrations of all the components . . . [as to] the term "component" and "phase" it will here suffice to say that in general the number of components increases as the number of separate chemical individuals increases, and that a phase is any solid, liquid or gaseous part of the whole system which possesses homogeneity of composition. For instance, if a system is made up of sand, salt solution, ice and aqueous vapor, each of these separate parts in that it is homogenous, is a phase. . . . Other things being equal, the greater number of phases, the less the tendency to change.

The quantitative character of this rule makes its application one of great difficulty, but it will serve as a guide or model for the organization of problems, and suggests the form into which experimental data should be organized, and secured for testing its application and validity.

The following extracts from Findlay ('04, pp. 8–18) will assist in gaining some of the general ideas involved in this subject:

> A heterogenous system is made up of different portions, each in itself homogeneous, but marked off in space and separated from the other portions by bounding surfaces. These homogeneous, physically distinct and mechanically separable portions are called *phases.* Thus ice, water, and vapor, are three phases of the same chemical substance—water. A phase, however, whilst it must be physically and chemically homogeneous, need not necessarily be chemically simple. . . . The *number of phases* which can exist side by side may vary greatly in different systems. In

all cases, however, there can be but one gas or vapor phase on account of the fact that all gases are miscible with one another in all proportions. In the case of liquid and solid phases the number is indefinite, since the above property does not apply to them. . . . It is important to bear in mind that equilibrium is *independent of the amounts* of the phases present.

By component (p. 10) is

meant only those constituents, the concentration of which can undergo *independent* variation in the different phases, and it is only with these that we are concerned here. . . . The Phase Rule is concerned merely with those constituents which take part in the state of real equilibrium; for it is only to the final state, not to the processes by which that state is reached, that the Phase Rule applies. (Pp. 11–13.) It is, however, only in the case of systems of more than one component that any difficulty will be found; for only in this case will a choice of components be possible. . . . Now, although these constituents take part in the equilibrium, they are not all to be regarded as components, for they are not mutually independent. . . . In deciding the number of components in any given system, not only must the constituents chosen be capable of independent variation, but a further restriction is imposed, and we obtain the following rule: *As the components of a system there are to be chosen the* SMALLEST NUMBER *of independently variable constituents by means of which the composition of each phase participating in the state of equilibrium can be expressed in the form of a chemical equation.* . . . Another method may be given by which the number of components present in a system can be determined. Suppose a system consisting of several phases in equilibrium, and the composition of each phase determined by analysis. If each phase present, regarded as a whole, has the same composition, the system contains only one component, or is of the first order. If two phases must be mixed in suitable quantities in order that the composition of a third phase may be obtained, the system is one of two components or of the second order; and if three phases are necessary to give the composition of a fourth coexisting phase, the system is one of three components, or of the third order. . . . Again, therefore, we see that, although the number of the components of a system is definite, a certain amount of liberty is allowed in the choice of the substances; and we also see that the choice will be influenced by the conditions of experiment.

Summing up, now, we may say:

1. The components are to be chosen from among the constituents which are present when the system is in a state of true equilibrium, and which take part in that equilibrium.

2. As components are to be chosen the *smallest number* of such constituents necessary to express the composition of each phase partici-

pating in the equilibrium, zero and negative quantities of the components being permissible.

3. In any given system the *number* of the components is definite, but may alter with alteration of the conditions of experiment. A certain freedom of choice, however, is allowed in the (qualitative, not quantitative) selection of the components, the choice being influenced by considerations of simplicity, suitability or generality of application.

We see, therefore, that in case of some systems two, in other cases, only one of the independent variables (temperature, pressure, concentration) can be altered without destroying the nature of the system; while in other systems, again, these variables have all fixed and definite values. We shall therefore define the number of degrees of freedom of a system as the *number of the variable factors, temperature, pressure, and concentration of the components, which must be arbitrarily fixed in order that the condition of the system may be perfectly defined.*

A knowledge of its variability is, therefore, of essential importance in studying the condition and behavior of a system, and it is the great merit of the Phase Rule that *the state of a system is defined entirely by the relation existing between the number of components and the phases present,* no account being taken of the molecular complexity of the participating substances, nor any assumption made with regard to the constitution of matter. It is, further, as we see, quite immaterial whether we are dealing with "physical" or "chemical" equilibrium; in principle, indeed, no distinction need be drawn between the two classes, although it is nevertheless often convenient to make use of the terms, in spite of a certain amount of indefiniteness which attaches to them—an indefiniteness, indeed, which attaches equally to the terms "physical" and "chemical" process.

The Phase Rule of Gibbs, now, which defines the condition of equilibrium by the relation between the number of coexisting phases and the components, may be stated as follows: A system consisting of n components can exist in $n+2$ phases only when the temperature, pressure, and concentration have fixed and definite values; if there are n components in $n+1$ phases, equilibrium can exist while one of the factors varies, and if there are only n phases, two of the varying factors may be arbitrarily fixed. This rule, the application of which, it is hoped, will become clear in the sequel, may be very concisely and conveniently summarized in the form of the equation—

$$P+F=C+2, \text{ or } F=C+2-P$$

where P denotes the number of the phases, F the degrees of freedom, and C the number of components. From the second form of the equation it can be readily seen that the greater the number of the phases, the fewer are the degrees of freedom. With increase in the number of phases, therefore, the condition of the system becomes more and more defined, or less and less variable. . . .

Systems which are apparently quite different in character may behave in a very similar manner. Thus it was stated that the laws which govern the equilibrium between water and its vapor are quite analogous to those which are obeyed by the dissociation of calcium carbonate into carbon dioxide and calcium oxide; in each case a certain temperature is associated with a definite pressure, no matter what the relative or absolute amounts of the respective substances are. And other examples were given of systems which were apparently similar in character, but which nevertheless behaved in a different manner. The relations between the various systems, however, became perfectly clear and intelligible in the light of the Phase Rule. In the case first mentioned, that of water in equilibrium with its vapor, we have one component—water—present in two phases, *i. e.*, in two physically distinct forms, viz., liquid and vapor. According to the Phase Rule, therefore, since $C=1$, and $P=2$, the degree of freedom F is equal to $1+2-2=1$; the system possesses one degree of freedom, as has already been stated. But in the case of the second system mentioned above there are two components, viz., calcium oxide and carbon dioxide, and three phases, viz., two solid phases, CaO and $CaCO_3$, and the gaseous phase, CO_2. The number of degrees of freedom of the system, therefore, is $2+2-3=1$; this system, therefore, also possesses one degree of freedom. We can now understand why these two systems behave in a similar manner; both are univariant, or possess only one degree of freedom. We shall therefore expect a similar behavior in the case of all univariant systems, no matter how dissimilar the systems may otherwise appear. Similarly, all bivariant systems will exhibit analogous behavior; and generally, systems possessing the same degree of freedom will show a like behavior. In accordance with the Phase Rule, therefore, we may classify the different systems which may be found into invariant, univariant, bivariant, multivariant, according to the relation which obtains between the number of the components and the number of the coexisting phases; and we shall expect that in each case the members of any particular group will exhibit a uniform behavior. By this means we are enabled to obtain an insight into the general behavior of any system, so soon as we have determined the number of the components and the number of the coexisting phases.

In the preceding quotations there are certain points to which special attention should be called:

1. The phase rule is concerned with equilibria, and not with the processes by which this state is reached. It thus supplements Bancroft's law in a very important manner, because that law is mainly concerned with the process of developing equilibria. To make complete continuity and

contact between these two methods and to fuse them into *one cycle* Bancroft's should also be quantitatively expressed (the interacting systems). The importance of this is evident. I have not seen attention called to this fact, or the intimate relation between these two laws.

2. The number of components, phases, independent variables, concentrations, etc., to which the phase rule applies, is also one of the most marked features of biological problems in its dealing with the relation of animals to diverse environmental conditions and media.

3. The analysis of biological problems into cycles of action, systems, and agencies, is a necessary simplification of the biological problems, and is preliminary to the determination of the number of components, phases, and concentrations which are involved in the application of the phase rule to equilibria, and to Bancroft's law of their development. Even in case of biological problems which have not been reduced to quantity this model of dynamic relations should be of much assistance in clarifying working plans, especially in associational studies.

4. Improvements in the dynamic theory will probably simplify its application to biology. The detailed nonmathematical expression of these correlations will facilitate their wider use in biology, and it is also equally evident that with an adequate mathematical equipment the biologist's application of these ideas would be greatly facilitated.

The phase rule has been so valuable chemically that a special effort should be made to use it as much as possible as a model in biological work. Mellor ('04, pp. 183–184) says: "Gibbs' phase rule is the best system extant for the classification of equilibria—chemical and physical. All changes, both physical changes of state and changes of chemical composition, are found to depend upon the same general laws." Henderson ('13, p. 260) remarks: "There can be no doubt that, when feasible, the ideal method—from the physico-chemical point of view—to de-

scribe a material system is in terms of the phase rule.''[8]

To apply these principles to the interaction of systems is the great practical problem. It requires, as previously mentioned, the analysis of the problem to such a degree as to distinguish its different systems and homogeneous units, their degrees of freedom, their directions of change, their cycles, their dynamic status and their quantitative relations. Many of these action systems have long been clearly recognized by plant and animal physiologists and ecologists, as cells, tissues, organs and communities, and many are recognized also in the physical and chemical world, where much attention is given to dynamic relations.

The processes of integration and dominance tend to limit this diversity of systems. It is believed, however, that to strive consciously for the application of these conceptions with some idea of what they imply, will, however, greatly hasten progress. Further, by calling attention to these general ideas it may enable some investigators to become better prepared for handling them, because we may well recall Pasteur's remark that: ''In the fields of observation chance favors only the mind which is prepared.'' It is hoped that by emphasizing these relations others better qualified than I am will give attention to this subject, and supply numerous examples in the various specialties; for it is by this method largely that others can become interested and extend the applications.

Up to this point the discussion has been mainly devoted to the development of a dynamic conception of systems and their methods of interaction. The migration of animals has long been recognized to include not only those caused by the activities of the animal itself, but also by the activity or agency of their environment; it is there-

[8] Henderson ('13) does not mention Bancroft's law or attempt to relate it to the phase rule. In my ''Guide'' ('13, p. 85) special attention was called to both Bancroft's law and the phase rule by listing these first among papers on dynamics. Recently, since this paper was written, I have seen Henderson's ('17, p. 138) criticism of Spencer's ''stability of the homogeneous,'' to which he applies the phase rule and refers also to Bancroft's law, although not as here advocated.

fore now necessary to review briefly some of the main environmental agencies and processes operative. The geologists and physiographers have made much progress in the dynamic interpretation of their problems, so that it is a relatively simple matter to adapt their results to our purpose. They have shown that the rocks below the ocean are heavier than those of the land and that the present shores of the oceans change as a dynamic equilibrium is established between the heavier sea bottom and the lighter land area (Willis, '11). We have in this a cause for innumerable changes in the physical features of the earth's surface, and in the environments of animals. This beautifully illustrates the fundamental unity and method of interaction between the liquid sea and the solid land systems. This is one of the huge physical cycles which illustrate every dynamic phase, from a condition of stress through the slow process of adjustment to strain —retarded by the rigidity of the earth's crust—on to a dynamic equilibrium. All the land area which remains above sea level is exposed to waves, the disintegrating influences of the atmosphere, and the erosion by wind and running water, all of which tend to cut down all land to sea level, and to deposit the heavy débris on the sea bottom, thus cumulatively destroying its relative equilibrium, and, supplemented by radio-activity, there are instituted cycles of stress, in an unending series.

In the equilibria existing between the land and the sea, the isotatic cycle, and the cycle of erosion or base-leveling, are found two phases of the most important gross influences in the physical causes of animal migration (cf. Woodworth, '94; Adams, '01). To this must be specifically included climatic cycles (Huntington, '14, and others) whose influence upon animal migration is also profound. Intimately related to the preceding physical factors are the cyclic changes in the vegetational covering of the earth, particularly those recognized in recent years by the plant ecologists (Cowles, '11; Clements, '16, and others). The physical changes influence all organisms,

and operate in both short and long cycles, the various cycles traveling at diverse rates and mutually influencing one another in their adjustments to pressure. In these wonderful moving systems of cycles can be visualized the essence of modern scientific conceptions. From electrons, atoms, molecules, chemical compounds, colloids, cells, tissues, organs, individuals, and culminating in the community and association, is seen in each a dynamic center or microcosm, about which revolves other systems, in turn revolving as a part of a larger system in ever widening expansion, each in turn subordinated to a higher order of dominance, the culmination of interacting systems.

I have now completed an outline of the fundamental dynamic principles which are necessary as a background for my discussion of animal migration. These general principles appear to underlie all processes of animal regulation internal and external, and are expressions of these laws of interacting systems.[9]

[9] Although the preceding discussion is intended to bear mainly on migration, it should not be inferred that I would limit it in this manner. It is my belief that these general principles are of relatively wide application.

(*To be continued*)

A STUDY OF HYBRIDS IN EGYPTIAN COTTON

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INTRODUCTION

THE Egyptian type of cotton comprises numerous varieties which have presumably originated by mutation (Kearney, 1914). This presumption is based upon the following facts:

1. Each variety descended from a single individual which differed in several characters from the parent form.

2. The absence or extreme rarity of connecting forms and the infrequency of sterility in both the parental and the mutant stock make it difficult to account for these mutants on the basis of recombination, as ordinarily understood.

3. The new characters of the mutant are uniformly expressed in the successive generations of its offspring as long as hybridization with other forms is excluded.

The observed facts make it difficult to escape the conclusion that these mutants are the result of simultaneous alteration of several factors in the egg cell after fertilization.[1] Otherwise, it is necessary to assume that the mutant has resulted from the union of a male and a female gamete, in both of which similar but independent alteration had taken place with respect to several factors. Probability is so greatly against this interpretation as to make it almost unthinkable.

The question suggests itself, what are the conditions under which mutation occurs in Egyptian cotton? The appearance of mutants has thus far been observed only in mixed stocks (Kearney, 1918, pp. 60–61). Hence, not-

[1] A case of mutation has been thus explained by Hayes and Beinhart (1914).

withstanding the difficulty of interpreting the mutants as direct recombinations, the inference can scarcely be avoided that mutation in this group is conditioned by heterozygosity.

In an endeavor to obtain more definite information on this point it was decided to make simple and back-crossed hybrids between two varieties of Egyptian cotton and to study these hybrids in comparison with line-bred progenies of the parent varieties. Mutants in this group are of comparatively rare occurrence, nothing analogous to the "mass mutation" observed by Bartlett (1915) in *Œnothera* and by De Vries (1918) in *Zea* having been observed. Very large numbers of plants of the hybrid and parental stocks will therefore need to be examined before we may hope to obtain reliable statistics as to the production of mutants. In the meantime, it is believed that what has been learned in regard to the behavior of these hybrids in the first three generations is of sufficient interest to warrant preliminary publication.

Most previous studies of hybrids in the genus *Gossypium* have been made upon interspecific crosses, such as Sea Island cotton (*G. barbadense*) × Upland cotton (*G. hirsutum*) and Egyptian cotton[2] × Upland cotton. In these cases there is very great variability in the F_2 and later generations. Cotton breeders have found it to be practically impossible to "fix" such hybrids, even after selection continued during six or seven generations. On the other hand, little is known of the behavior of crosses between varieties within the same species. Are such hybrids less variable and less difficult to fix by selection, and, if so, can not stable and uniform new varieties be obtained by recombination? It is believed that these questions are partly answered by the data presented in this paper.

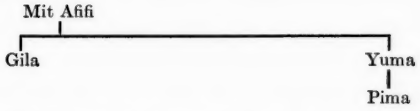
The investigation was conducted at the Cooperative Testing Garden, Sacaton, Arizona, which is conducted

[2] The Egyptian type of cotton, although commonly supposed to be of hybrid origin (Balls, 1912, pp. 3, 4) presents many analogies to a natural species and its differences from American Upland cotton are certainly of specific magnitude.

by the Bureau of Plant Industry in cooperation with the Indian Service. The writers are indebted to Mr. G. N. Collins of the Bureau of Plant Industry for many helpful suggestions throughout the course of the investigation.[3]

Plan of the Investigation

The only varieties of Egyptian cotton of which approximately pure strains were available when the experiment was begun were the Yuma, Gila and Pima varieties, all of which had been developed in Arizona. These varieties were described (with illustrations of the leaves, bracts, and bolls) and an account of their origin was given in an earlier publication (Kearney, 1914). Their relationship may be indicated thus:



The Gila and Pima varieties were chosen because they show the greatest amount of difference in the largest number of characters. Of the three varieties, Gila is most similar to the common ancestor, Mit Afifi, and Pima is the most distinct from it. Gila may, in fact, be regarded as representing a small portion of the area of variation of the extremely heterozygous Mit Afifi stock from which all these varieties have descended, while the characters of Pima are far outside the hitherto observed range of variation in Mit Afifi. The hybrids described in this paper may therefore be taken to represent, in a measure, the result of crossing the mutant Pima with its more remote ancestor, Mit Afifi.

Several typical individuals of each variety were selected in July, 1914. A number of flowers were self-pollinated on each plant and intervarietal cross-pollinations were made among them. The resulting first gen-

[3] It is not practicable to publish in full the voluminous data resulting from this investigation but the writers are prepared to supply, to any one who may be interested, photographic copies of the original records, at the cost of reproduction.

eration parental and hybrid progenies were grown in 1915. Seeds produced by flowers which were selfed on certain individuals in these progenies furnished the second generation, which was grown in 1916. Flowers on selected plants in the second generation parental and F_2 hybrid progenies were again selfed to furnish the third generation parental and the F_3 hybrid progenies, which were grown in 1917.

Some of the flowers on F_1 hybrid plants in 1915 were pollinated from plants in the first generation progenies of the original parent plants of either variety. From the resulting seed $\frac{3}{4}$ Pima and $\frac{3}{4}$ Gila back-crosses were grown in 1916. Plants were selected in each of the $\frac{3}{4}$ back-cross progenies because of their approach to the corresponding predominant parent in respect to important characters. The Pima back-cross plants were pollinated from a plant in the second selfed generation of the Pima parent and the Gila back-cross plants were pollinated from a similar Gila individual. The resulting $\frac{7}{8}$ Pima and $\frac{7}{8}$ Gila back-cross progenies were grown in 1917.

Every effort was made to grow the various parental and hybrid progenies under as nearly as possible uniform conditions in respect to soil, irrigation and cultural treatment. All comparisons of hybrids and parents have been made on the basis of progenies grown the same season, in order to obviate the influence of different weather conditions. Measurements on the different plants were made, as far as practicable, upon organs which occurred at the same nodes of the axis and branches and which were in the same stage of development. The number of plants on which most of the characters were measured in each generation were, in round numbers:

	F_1 (1915)	F_2 (1916)	F_3 (1917)
Pima	60	200	180
Gila	40	200	100
Pima × Gila	80	400	300

Characters Measured and Significance of the Varietal Differences

The Pima and Gila varieties, as represented by the first and second generation progenies of the selected parent individuals, differed by an amount equal to three or more times the probable error of the difference, in respect to 24 characters. Many of these are physically or physiologically correlated, but six of the characters showed practically no correlation inter se, in either parent. Most of these characters are expressions of size (*e. g.*, the length of the internodes, leaves, floral parts, bolls and fiber) or are ratios between two size characters and expressive of shape. The leaf index $\frac{\text{length}}{\text{width}} \times 100$ and the boll index $\frac{\text{length}}{\text{diameter}} \times 100$ showed especially significant differences between the two varieties named, the difference in the second generation having been 26 times the probable error in respect to leaf index and 46 times the probable error in respect to boll index. In length of fiber the difference between the parents in the second generation was 22 times its probable error. The only characters of diagnostic value which could not be accurately measured and which were therefore determined by grading, were color of the fiber,[4] amount of fuzz on the seeds and roughness of the boll surface (depending upon the depth, number and regularity of distribution of the pits in which the oil glands are situated). Even in respect to these characters the differences were of degree rather than of kind.

The Gila variety, as represented by three successive selfed generations of the progenies of the parent plants, gave larger coefficients of variation for most of the characters than did the Pima variety. Since no general decrease in the variability of either variety was observed after three generations of selfing, it would appear that Gila is inherently more variable than Pima.

The two varieties, as represented by the first and sec-

[4] The two varieties showed no difference in the color of any part of the flower.

ond generation progenies of the plants selected as parents of the hybrids, showed overlapping ranges for all characters excepting fuzziness of the seed and color of the fiber. These two characters were measured on only small numbers and overlapping would very likely have been observed if larger populations had been compared.

THE SIMPLE HYBRIDS

Means

Comparing the means of the simple hybrids (Pima × Gila) with those of the parents, a strong tendency to intermediacy was apparent. The means for a large majority of the characters, in both the F_1 and F_2, lay between the parental means, and in nearly one half of the total number of characters the hybrid means did not differ significantly from the midpoint of the parental means. The relative number of characters for which the departure of the hybrid mean was towards the Pima mean was much greater in the F_1 than in the F_2. This was probably due to increased vigor in the conjugate generation, eight of the thirteen characters which showed a significant[5] departure of the hybrid F_1 mean from the midpoint of the parents being size characters for which the Pima parent gave a larger mean than the Gila parent.

Eleven F_3 progenies of the simple hybrid were grown in 1917 from plants which were selected in the F_2 in 1916 because of their approach to one or the other parent or because of their intermediacy with respect to various characters, especially leaf index and boll index. The F_3 means for these characters in all cases fell between the means of the third generation parental progenies, or else did not differ significantly from the mean of one or the other parent.

Coefficients of Variation

In all three generations the hybrids gave significantly larger coefficients of variation, for most of the characters,

[5] A difference or other quantity is here referred to as "significant" when amounting to three or more times its probable error.

than did the corresponding selfed parental progenies of the Pima variety, but were not significantly more variable than the corresponding Gila progenies. In length of fiber the hybrid F_2 was not significantly more variable than either parent. The hybrid F_2 was significantly more variable than the F_1 in the leaf characters, but not in the boll characters. This result was so surprising that it was accepted only after repeatedly checking the original data. The averages of the coefficients of variation, for leaf index and boll index, of the eleven F_3 hybrid progenies did not differ significantly from the coefficients of the F_2 progeny from which they were derived. The average variability of the F_3 did not exceed that of the third selfed generation of the more variable parent (Gila) and two of the F_3 progenies were not more variable than the corresponding generation of the less variable parent (Pima).

These facts point to the possibility of obtaining a relatively uniform new variety of cotton by hybridization of two varieties belonging to the same general type, although hybrids between different types, such as Egyptian and Upland, are notoriously difficult to fix.[6]

Distributions

The distributions, for the important characters leaf index, boll index and fiber length, of the parental and simple hybrid progenies, are shown in Figs. 1 to 3.

The range of the hybrid F_2 for none of the characters appreciably exceeded the combined parental ranges and for the majority of characters it was more restricted than the latter. The variation was therefore much smaller than in the F_2 of hybrids between less closely related types of cotton, in which the range often greatly exceeds that of both parents. (For example, the Egyp-

[6] Longfield Smith (1915, p. 30) states that hybrids between the not very dissimilar Sea Island and Sakellaridis cottons were "fairly uniform" in the F_2 and F_3. Different behavior was shown by the cross between Sea Island and "St. Croix Native," a type more nearly resembling American Upland cotton. In this case, "new characters, not present in either of the original plants, appear in the first and subsequent generations," and the F_2 and F_3 "split into a mass of types."

tian × Kekchi hybrids described by Cook (1909, p. 12–14) and the Egyptian × Hindi hybrids described by Marshall (1915).)

Little or no evidence of dominance was shown by the distributions, for the various characters, of the F_1 of the

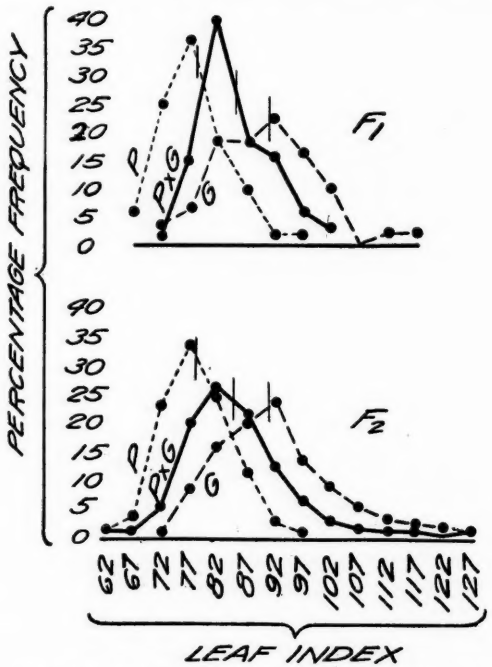


FIG. 1. Leaf index: first and second generation distributions of the parental and simple hybrid progenies. The dotted line curve represents the distribution of the Pima parent, the broken line curve that of the Gila parent and the solid line curve that of the hybrid. The short vertical line on each curve indicates the location of the mean of that population. The figures on the axis of ordinates indicate the number of plants in each class, taken as a percentage of the total number of the population. The figures on the axis of abscissas indicate the classes.

The actual numbers of the respective populations were: F_1, Pima 60, Gila 40, P × G 80; F_2, Pima 213, Gila 203, P × G 418.

simple hybrids. The F_2 distributions were strictly unimodal for all characters excepting the highly variable one length of axis, and even in this case the indication of bimodality was so slight as to be probably insignificant.

No evidence of segregation in definite ratios was obtained.

It is well known that complete dominance in the F_1 and 3:1 segregation in the F_2 are exceptional in size and shape characters such as chiefly distinguished the Pima and Gila varieties of cotton. On the other hand, the question whether the behavior of the Pima × Gila hy-

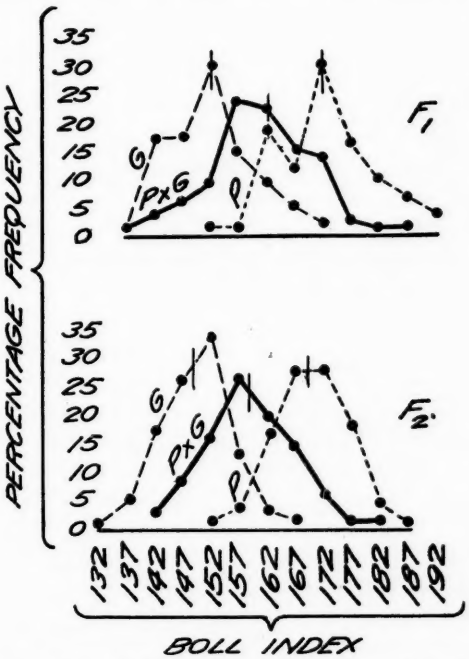


FIG. 2. Boll index: first and second generation distributions of the parental and simple hybrid progenies. Details as in Fig. 1. The actual numbers of the respective populations were: F_1, Pima 60, Gila 40, P × G 80; F_2, Pima 161, Gila 207, P × G 419.

brids with respect to such characters might be interpreted by the multiple factor hypothesis is extremely difficult to answer. The differences between the means of the parents for most of the characters, while small, are highly significant, but the parental ranges, in most cases, overlap to such an extent that Mendelian analysis would seem to be out of the question.

A few of the characters in respect to which these varieties differ significantly might be termed "qualitative." These are roughness of the boll surface, color of the fiber and fuzziness of the seed, all of which are included in the lists of allelomorphic pairs of characters in cotton

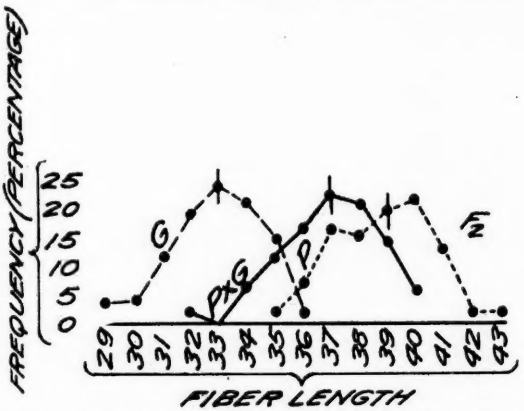


FIG. 3. Fiber length (mm.); second generation distributions of the parental and simple hybrid progenies. Details as in Fig. 1. The actual numbers of the respective populations were: Pima 46, Gila 53, P × G 49.

given by Balls (1909, p. 18) and by McLendon (1912, pp. 168, 169).[7] Yet in the Pima × Gila hybrids these characters behaved like the size and shape characters, showing unimodal distribution in the F_2. It should be noted, however, that in respect to these characters the differences between the two Egyptian varieties are much smaller than the differences between the parents of the wider crosses (Egyptian × Upland and Sea Island × Upland) dealt with by Balls and McLendon. Instead of the differences between pitted and smooth bolls, buff and white fiber and smooth and fuzzy seeds we have, in comparing Pima with Gila, merely the differences between more and less numerously and regularly pitted bolls, lighter and darker buff-colored fiber and more and less fuzz on the seeds.

[7] Complete dominance is apparently a rather rare phenomenon in cotton, even in the case of color characters. It is stated, however, by Leake and Prasad (1914, pp. 126–128) that yellow corolla color and the presence of the petal spot are completely dominant in certain hybrids of Indian cottons.

Correlation of Characters

It was sought to ascertain whether these hybrids show genetic as distinguished from merely physical or physiological correlations, in other words, whether there is coherence in the transmission of the parental characters. To this end, application was made of the test proposed by Collins (1916, p. 439), *i. e.*, comparison of the coefficients of correlation of the F_2 with those of the F_1. It is assumed that if the F_2 coefficient significantly exceeds that of the F_1, in the direction indicated by the relation of the parental means for the two characters, genetic correlation or coherence of characters is indicated. For example, the Pima parent has a lower leaf index and a higher boll index than the Gila parent. If there is coherence of these characters, the hybrid should show a negative correlation and the coefficient of correlation should be significantly larger in the F_2 than in the F_1.

The coefficients of correlation of 40 pairs of characters were determined for both the F_1 (grown in 1915) and F_2 (grown in 1916), upon the basis of one measurement of each character on each plant.[8] In three of these cases the coefficient of correlation of the F_2 was significantly larger than that of the F_1 (difference from 3.5 to 4.5 times its probable error), in the direction indicated by the parental relation. Since, however, the coefficients of correlation of the first generation (1915) and second generation (1916) of the parental progenies had also been found to differ in magnitude, the possibility was considered that the difference in the F_1 and F_2 hybrid coefficients was at least partly due to variations in the weather of the two years. The coefficients of correlation for the three character pairs above mentioned were therefore calculated for a new F_1 which was grown in the same year as the F_2.[9] When the F_2 and the new F_1 coefficients

[8] Two characters of great practical importance and in respect to which the parents differ very significantly, length of fiber and fuzziness of seeds, showed no significant correlations, either with each other or with the leaf and boll characters.

[9] The new F_1 was the result of crosses between daughters of the original parent plants, which had been made in 1915.

were compared, it was found that the former was significantly larger than the latter, in the indicated direction, for only one pair of characters (width of leaf and number of teeth on the involucral bracts) and in this case the difference was only 3.2 times its probable error.[10]

It was sought to throw further light upon this problem by determining the coefficient of correlation in the hybrid upon the basis of progenies rather than of individual plans. The means, for leaf index and boll index, of eleven F_3 hybrid progenies were used for this purpose. These progenies comprised from 8 to 44 plants each and the means were based upon measurement of one leaf and one boll on each plant. Since the Pima parent has the smaller leaf index and the larger boll index, the correlation in the hybrid, if determined by the parental relations of the two characters, should be negative. The coefficient obtained was in fact negative, but was no larger than its probable error ($r = -.17 \pm .18$).[11]

The balance of evidence is therefore strongly against the occurrence of coherence of characters in these hybrids between somewhat closely related, although distinct, varieties of cotton. It does not, of course, follow that the same result would have been obtained in the case of hybrids between less closely related types, especially if these differ in allelomorphic characters rather than in the variable size and shape characters which chiefly distinguished Pima from Gila.[12]

[10] The correlation in question, width of leaf with number of teeth on the involucral bracts, is doubtless physiological, large bracts being associated with large leaves and the number of teeth being greater on the larger bracts.

[11] The existence of an intervarietal correlation by no means implies that the same correlation will be found to obtain within a variety. For example, it is a matter of common observation that most varieties of cotton which have very long fiber have relatively sparse fiber, and vice versa. But when the correlation between fiber length and lint index (weight of fiber per 100 seeds) was plotted for 80 plants of the Pima variety, the value of r was found to be only $.07 \times .07$, showing the complete absence of an intravarietal correlation.

[12] Instances of coherence of characters in hybrids of Egyptian with Upland cotton have been reported by Cook (1909, pp. 16, 17 and 1913, p. 53). On the other hand, Marshall (1915, pp. 57, 61), describing the F_2 of hybrids

The Back-Crossed Hybrids

The means of the ¾ back-crossed hybrids for nearly all characters showed departures from the midpoint of the parental means which were both significant and towards the mean of the respective preponderant parent (Pima or Gila). In the ⅞ back-crosses, the mean virtually coincided with those of the preponderant parent, as the following data show:

Progeny Means of:	Leaf Index	Boll Index
Pima	78.1 ± .14	173 ± .18
Pima ⅞ back-cross [(P × G) × P] × P	78.7 ± .63	179 ± .66
Gila ⅞ back-cross [(P × G) × G] × G	94.1 ± .47	153 ± .90
Gila	93.1 ± .47	156 ± .51

The distributions, for leaf index and boll index, of the Pima ⅞ back-cross, were embraced by those of Pima and the distributions of the Gila ⅞ back-cross were embraced by those of Gila. It is therefore apparent that twice back-crossing the simple hybrid with either of its parents has sufficed to eliminate the influence of the other parent in the expression of these characters.

Absence of Mutants

Careful examination, in 1916, of every plant in the F_2 progenies of the simple hybrids and in the ¾ back-cross progenies, showed only various recombinations of the Pima and Gila characters. A large majority of the simple hybrid plants were approximately intermediate, although occasional individuals showed a near approach to one or the other parent. Most of the back-cross plants, as compared with the simple hybrid individuals, showed clearly the preponderating influence of the ¾ parent, but few if any plants in the ¾ back-cross progenies could have been classed as wholly Pima or wholly Gila, the influence of the one-quarter parent being observable in the great majority of cases. No instance of

between the equally different Egyptian and Hindi cottons, states: "Nor was it possible to discover any general correlations or definite associations between any of the more important structural differences."

the occurrence of new or extra-parental characters was detected, although a few plants in the F_2 of the simple hybrid slightly exceeded the range of one or the other parent. Examination, in 1917, of the F_3 progenies of the simple hybrids, and of the $\frac{7}{8}$ back-cross progenies also failed to reveal the occurrence of any extra-parental characters. Nor have any new characters been detected in the first, second or third generation progenies from selfed seed of the parent individuals. It is evident, therefore, that nothing in the nature of a mutant has yet appeared in any of these line-bred and hybrid stocks.

It was not, however, expected that mutants would be detected in these small progenies, which were grown for the purpose of studying, under controlled conditions, the behavior of the hybrids in the earlier generations and to provide seed for the growing of each stock on a more extensive scale. Statistical evidence regarding the production of mutants can scarcely be expected until much larger numbers of plants have been examined. The stocks resulting from repeated back-crossing should be especially interesting to study in regard to the occurrence of mutation.[13]

CONCLUSION

The investigation here described was undertaken in the endeavor to ascertain the conditions under which mutants are produced, in Egyptian cotton. Simple and back-crossed hybrids were made between two varieties (Pima and Gila) which differ significantly in numerous characters. Three generations of the hybrid progenies and of progenies from selfed seed of the parent individuals, were grown. No evidence of the appearance of

[13] "Variations toward Upland or Hindi characters arising in dilute hybrid stocks of Egyptian cotton have been found to yield progenies with more stable expression of characters than direct hybrids between Egyptian and Upland cotton. Such facts suggest the possibility of developing a new method of breeding by dilute hybridization. By the use of a small proportion of foreign blood as a means of inducing mutative variations in otherwise uniform stocks it may be possible to secure desired combinations of characters in more stable form than they can be obtained by direct hybridization." (Cook, 1913, p. 96.)

new characters was detected in any of these progenies, but since mutants in Egyptian cotton are comparatively rare, it will doubtless be necessary to examine much larger populations before definite conclusions can be drawn as to the occurrence of mutation in these stocks.

The principal interest of the data thus far obtained attaches to the behavior of hybrids between varieties belonging to the same general type, as compared with that of the hybrids between different species of *Gossypium*, which have hitherto been the principal subject of genetic investigation in this group of plants.

The varieties used in this investigation are distinguished chiefly by size and shape characters, although a few of the characters in which they differ significantly have been found to behave as allelomorphs in hybrids between less nearly related forms of *Gossypium*. The Pima $\times$ Gila hybrids, however, showed no evidence of segregation in definite ratios in respect to any of the characters measured. There was little or no evidence of dominance in the F_1, and the F_2 distributions were practically without exception unimodal. The means of the simple hybrid were in most cases intermediate between those of the parents. The result of twice back-crossing the simple hybrid upon either parent was to obliterate the expression of the characters of the other parent.

It could not be demonstrated that genetic correlation or coherence of characters occurs in these hybrids. Apparently all characters which are not correlated physically or physiologically are transmitted independently.

The second and third generations of the hybrids, as compared with the parents after two and three generations of selfing, were not more variable than Gila, and were only a little more variable than Pima. This fact is of practical importance in cotton breeding, since it points to the possibility of obtaining relatively stable and uniform recombinations of the desirable characters of varieties belonging to the same general type, although breeders have found this to be well nigh impossible in

wider crosses such as those of Egyptian (or Sea Island) with Upland cotton.

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GENETIC RELATIONS OF THE WINGED AND WINGLESS FORMS TO EACH OTHER AND TO THE SEXES IN THE APHID MACROSIPHUM SOLANIFOLII

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INTRODUCTION

LIFE cycles are known, in many aphid species, from field observations alone. A number of cycles have been determined from breeding experiments upon aphids in confinement. Often, however, these experiments appear not to have used the pedigree method. In the course of some work on the potato aphid, *Macrosiphum solanifolii*,[1] I observed indications of peculiarities in the genetic relations of the various forms to each other, which could be detected only by the pedigree method. Experiments designed to demonstrate these relations were instituted, with the results described in this paper.

Macrosiphum solanifolii, as observed in these experiments, comprises four kinds of individual: (1) the apterous viviparous female, which is green; (2) the alate viviparous female, which is also green; (3) the oviparous or sexual female, which is wingless and of a yellowish-green color until late in life, when the abdomen becomes filled with green eggs which impart a green color to the female herself; and (4) the male, which is winged and of a brown or brown and green color. Of these types of individual, the alate female can be recognized when a little more than half grown by her wing pads. The oviparous female has thickened brown hind tibiæ covered with sensoria, which are recognizable with the unaided eye, and which develop a few days before maturity. The male

[1] Identified by Dr. Edith M. Patch.

is usually, though not always, distinguishable at birth because of its pink or gray color, and those that are green at birth usually develop the gray or pink color within a few days. This color of the immature male has not, I believe, been recorded in the published descriptions of the species, and it is not impossible that it is a characteristic of certain parthenogenetic lines only.

Miss Patch (1915) has described a pink variety of each of the viviparous forms. I have never seen these in my experiments, though thousands of individuals have been examined, except in diseased animals which died shortly after discovery. The immature pink aphids in my experiments have all been males. The occurrence of pink females is probably a characteristic of certain parthenogenetic lines.

In my experiments the potato has been exclusively used as the host plant. These plants were reared in pots and were covered with lantern globes closed at the top with muslin.

EXPERIMENTS

Relation of Winged and Wingless Forms to Each Other

Experiment 293.—Starting with sister individuals, two lines were bred for three generations, one line from apterous parents exclusively, the other from alate parents only. As in the other experiments to be described, about a dozen adult females were placed together on a single plant, to become parents of the following generation. When they began to produce young, the latter were removed daily, or every two days, to young plants. Successive groups of young were placed on one plant until they seemed likely to become too crowded (usually not over 150 per plant), after which a new plant was used. As many as five plants were required in some cases to receive the young of one lot of parents. In the tables these plants are designated, in the columns headed "Host Plant," as first, second, third, etc. As the young aphids became adult they were removed and either used for further breeding or destroyed.

As a rule the parents for the following generation were taken from the first of the host plants, and were transferred to a young healthy plant, on which they produced their young.

This particular experiment was started in June from a stock whose stem mother hatched in the greenhouse in the preceding January. The line had passed through a sexual phase in that time, but had been preserved by a small number of viviparous females. In Table I the line from apterous parents is represented in the upper half of the table, the line from alate parents in the lower half. For the sake of comparison the totals are placed together at the bottom of the table.

TABLE I

CONTRASTING THE OFFSPRING OF APTEROUS PARENTS AND THOSE OF ALATE PARENTS IN THE APHID *Macrosiphum solanifolii*

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	June 27–June 30	49	64	0	0
		Second	July 2	35	73	0	0
		Third	July 4–July 5	33	48	0	0
II....	Apterous	First	July 7–July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14–July 16	27	28	0	0
III...	Apterous	First	July 18–July 21	47	29	0	0
		Second	July 23	7	7	0	0
I.....	Alate	First	June 28–July 2	110	21	0	0
		Second	July 4–July 6	32	2	0	0
II....	Alate	First	July 9–July 11	66	29	0	0
		Second	July 13–July 14	99	50	0	0
		Third	July 16–July 18	62	52	0	0
		Fourth	July 21	41	12	0	0
		Fifth	July 23	14	4	0	0
III...	Alate	First	July 21	80	23	0	0
		Second	July 23	35	6	0	0
		Third	July 24–July 26	5	3	0	0
Totals from apterous parents.....				285	517	0	0
Totals from alate parents.....				544	202	0	0

There is a striking preponderance of winged offspring in the families of wingless parents, and a preponderance of wingless offspring from winged parents.

Experiment 294.—This was a repetition of the preceding experiment, in part simultaneous with it but of shorter duration. The method of conducting the experiment was the same as in the preceding experiment. Table II gives the results.

TABLE II

CONTRASTING TWO RELATED LINES OF *Macrosiphum solanifolii*, ONE REARED FROM APTEROUS PARENTS, THE OTHER FROM ALATE PARENTS

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	July 7–July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14–July 16	27	28	0	0
II....	Apterous	First	July 18–July 21	47	29	0	0
		Second	July 23	7	7	0	0
I.....	Alate	First	July 7–July 9	98	58	0	0
		Second	July 11	93	67	0	0
		Third	July 13	62	18	0	0
		Fourth	July 14–July 16	66	46	0	0
		Fifth	July 18	17	3	0	0
II....	Alate	First	July 18	65	10	0	0
		Second	July 21	179	29	0	0
		Third	July 23–July 24	22	4	0	0
Totals from apterous parents.....				168	332	0	0
Totals from alate parents.....				602	235	0	0

The conclusion is the same as from Table I. Apterous parents give birth more largely to alate offspring, alate parents more largely to apterous offspring.

Relation of Winged and Wingless Forms to the Sexes

Experiment 303.—Just before the sexual phase of the cycle began a line from winged parents was started from a line being reared from wingless parents. In so far as the two were bred simultaneously their progeny are recorded in Table III.

Of the sexual offspring, the wingless parents produced exclusively males, while the wingless parents gave birth to a very large majority of sexual females. It may be

TABLE III

CONTRASTING THE PROGENY OF ALATE PARENTS WITH THE PROGENY OF APTEROUS PARENTS, WITH SPECIAL REFERENCE TO THE SEXUAL FORMS, IN THE APHID *Macrosiphum solanifolii*

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Sept. 7–Sept. 9	68	2	0	0
		Second	Sept. 11–Sept. 13	33	37	0	0
		Third	Sept. 15–Sept. 19	0	14	0	36
		Fourth	Sept. 21	0	0	0	11
II....	Apterous	First	Sept. 21–Sept. 23	0	62	0	0
		Second	Sept. 25–Sept. 27	0	17	0	0
		Third	Sept. 29–Oct. 9	0	2	0	59
		Fourth	?	0	0	0	11
I.....	Alate	First	Sept. 17–Sept. 19	6	9	0	0
		Second	Sept. 21–Sept. 23	7	0	8	12
		Third	Sept. 25–Sept. 27	0	0	19	1
		Fourth	Sept. 29–Oct. 5	1	0	14	4
II....	Alate	First	Sept. 27–Sept. 29	0	0	27	0
		Second	Oct. 1–Oct. 7	0	0	62	0
		Third	Oct. 9	0	0	4	0
Totals from apterous parents.....				101	134	0	117
Totals from alate parents.....				14	9	134	17

also pointed out that the conclusion regarding the relation of the winged and wingless viviparous females to each other that was drawn from Tables I and II is confirmed in Table III.

Progressive Change in the Frequency of all the Forms in Successive Generations

Confirmation of the conclusions drawn from the preceding experiments is found in several lines which were designed to show the normal life cycle over a considerable period when each generation was derived from wingless parents. In addition, these lines show a progressive change in frequency of both the winged and wingless viviparous forms and of the sexes. Owing to this progressive change it was not possible to maintain uniform parentage, since in the late generations there were no apterous individuals from which to breed. The principal lines were obtained in the three following experiments.

Experiment 299.—This was a line reared from a wingless female obtained out of doors about August 10. It was reared in the laboratory. Table IV records this line.

TABLE IV

A PARTHENOGENETICALLY-PRODUCED LINE OF *Macrosiphum solanifolii*, PRODUCED IN THE MAIN BY WINGLESS PARENTS

Note (1) the gradual transition from wingless to winged viviparous females; (2) the transition from viviparous (parthenogenetic) reproduction to sexual reproduction; and (3) the fact that the males are produced mainly by wingless parents, the sexual females chiefly by winged parents. See Experiment 299.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Aug. 24–Aug. 25	50	0	0	0
		Second	Aug. 27–Aug. 28	51	0	0	0
		Third	Aug. 30–Sept. 3	29	0	0	0
II....	Apterous	First	Sept. 1	93	0	0	0
		Second	Sept. 3	149	0	0	0
		Third	Sept. 5–Sept. 7	49	0	0	0
		Fourth	Sept. 5–Sept. 15	0	2	0	37
		Fifth	Sept. 9–Sept. 15	58	42	0	7
		Sixth	Sept. 17	4	1	0	0
III...	Apterous	First	Sept. 9–Sept. 11	57	17	0	0
		Second	Sept. 13–Sept. 17	9	13	0	7
		Third	Sept. 19	0	0	0	9
IV...	Apterous	First	Sept. 17–Sept. 19	13	86	0	0
		Second	Sept. 21–Sept. 23	1	30	1	13
		Third	Sept. 25–Sept. 27	0	0	0	15
		Fourth	Sept. 29–Oct. 10	0	0	0	11
V....	Apterous	First	Sept. 27	6	81	0	0
		Second	Sept. 29	0	34	0	0
		Third	Oct. 1–Oct. 3	0	2	14	44
		Fourth	Oct. 5–Oct. 7	0	0	2	39
		Fifth	Oct. 9–Oct. 16	0	0	0	25
VI...	Apterous	First	Oct. 7–Oct. 9	2	17	3	0
		Second	Oct. 11–Oct. 16	0	1	11	21
		Third	Oct. 20–Oct. 27	0	0	0	12
	Alate	First	Oct. 16–Oct. 25	0	0	24	0
		Second	Oct. 30–Nov. 6	0	0	4	0
VII..	Apterous	First	Oct. 18–Oct. 30	0	5	11	3
		Second	Nov. 6	0	0	0	1
	Alate[2]	First	Oct. 18–Oct. 20	0	0	134	0
		Second	Oct. 23	0	0	101	0
		Third	Oct. 25–Oct. 27	0	0	44	0
		Fourth	Oct. 30–Nov. 6	0	0	18	0
VIII.	Alate[2]	First	Nov. 1–Nov. 3	0	0	50	0
		Second	Nov. 6	0	0	10	0
		Third	Nov. 10	0	0	3	0

[2] The alate parents in the seventh and eighth generations were offspring of apterous parents.

Experiment 298.—This line was derived from the same female as Experiment 299, but was reared in the greenhouse. See Table V.

TABLE V

A PARTHENOGENETICALLY PRODUCED LINE OF *Macrosiphum solanifolii*, PRODUCED CHIEFLY BY APTEROUS PARENTS.

The same transitions noted in Table IV are observable here on a smaller scale. See Experiment 298.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	Aug. 13	7	0	0	0
II....	Apterous	First	Aug. 15–Aug. 17	100	5	0	0
III...	Apterous	First	Aug. 24–Aug. 27	15	0	0	0
		Second	Aug. 28–Aug. 30	65	2	0	0
		Third	Sept. 1–Sept. 5	64	4	0	0
IV...	Apterous	First	Sept. 7–Sept. 9	68	2	0	0
		Second	Sept. 11–Sept. 13	33	37	0	0
		Third	Sept. 15–Sept. 19	0	14	0	36
		Fourth	Sept. 21	0	0	0	11
V....	Apterous	First	Sept. 21–Sept. 23	0	62	0	0
		Second	Sept. 25–Sept. 27	0	17	0	0
		Third	Sept. 29–Oct. 9	0	2	0	59
		Fourth	?	0	0	0	11
V ...	Alate	First	Oct. 13–Oct. 20	0	0	14	0
		Second	Oct. 23	0	0	4	0

Experiment 270.—The stem mother of this line hatched from a fertilized egg that was laid in the greenhouse in November and hatched in January. In March and April the line passed through a sexual phase, but a small number of viviparous females were produced during this period and by them the parthenogenetic line was continued. The families were not fully recorded until the latter part of May. Table VI includes only the records beginning May 28. Nine generations are there recorded as if an uninterrupted line, but an explanation is necessary. In the midst of the fifth generation the aphids began to die in large numbers for an unknown reason. In a few days every aphid out of hundreds was dead. Fortunately two or three aphids were found on a discarded plant in the greenhouse. Since only this one line had been reared in the greenhouse up to that time I felt

TABLE VI

A PARTHENOGENETIC LINE OF THE APHID *Macrosiphum solanifolii* REARED CHIEFLY FROM APTEROUS PARENTS

With certain irregularities the features mentioned in Table IV are recognizable here also. See Experiment 270.

Generation	Parents	Host Plant	Dates of Isolating Young	Offspring			
				Apterous Viviparous Females	Alate Viviparous Females	Oviparous (Sexual) Females	Males
I.....	Apterous	First	May 28–June 3	12	31	0	0
		Second	June 5–June 8	8	0	0	0
II....	Apterous	First	Juné 12–June 16	31	25	0	0
		Second	June 18–June 25	3	5	0	0
III...	Apterous	First	June 27–June 30	49	64	0	0
		Second	July 2	35	73	0	0
		Third	July 4–July 5	33	48	0	0
IV...	Apterous	First	July 7–July 9	22	118	0	0
		Second	July 11	44	88	0	0
		Third	July 13	21	62	0	0
		Fourth	July 14–July 16	27	28	0	0
V....	Apterous	First	July 18–July 21	47	29	0	0
		Second	July 23	7	7	0	0
VI...	Apterous	First	Aug. 17	7	0	0	0
VII..	Apterous	First	Sept. 1–Sept. 9	27	0	0	0
		Second	Sept. 11–Sept. 17	4	0	0	4
		Third	Sept. 19–Oct. 5	1	0	0	10
VIII .	Apterous	First	Sept. 21–Sept. 23	0	50	2	0
		Second	Sept. 25–Sept. 27	0	15	5	15
		Third	Sept. 29–Oct. 3	0	0	0	34
		Fourth	Oct. 5–Oct. 16	0	0	0	29
IX...	Alate	First	Oct. 11–Oct. 16	0	0	76	0
		Second	Oct. 18–Oct. 25	0	0	4	0

safe in assuming that these were of the same line. From one of them the sixth (?) and succeeding generations of Table VI were obtained.

Attention is directed in Tables IV, V, and VI to the following points:

1. The wingless viviparous females, more abundant early in the cycle, are gradually replaced by winged females. This is especially clear in Tables IV and V. It is obscured in Table VI by the fact that this line is not really a continuous one. A catastrophe in the fifth generation made it necessary to resume this line by means of a female from the same stock. Up to the fifth generation there is an irregular increase in the proportion of winged females, which reaches its climax in the fourth

generation. It is impossible to state what the fifth generation would have included, since only one fifth of the probable progeny were produced or survived. After the fifth generation up to the complete disappearance of viviparous forms, there was again a replacement—this time rather sudden than gradual—of the wingless females by winged ones. The same gradual disappearance of wingless viviparous in favor of winged females was observed in several other experiments of shorter duration which are not included in this paper, and has also been found in *Microsiphum destructor* by Miss Gregory (1917). It is therefore to be regarded as of general occurrence.

2. There is observed in two of the tables (IV and VI) a gradual increase in the tendency of wingless females to produce sexual females instead of males, as they most often do when the sexual phase begins. Thus in Table IV, generation IV, 2.5 per cent. of the sexual forms produced by apterous parents were sexual females. In generation V, 12.9 per cent. of the sexual forms were females. In the sixth generation, of the sexual offspring of apterous parents, 29.7 per cent. were females. In the seventh generation, which is the last from apterous parents, 73.3 per cent. of the sexual offspring were females. Thus, while the apterous parents produced mostly males during the sexual phase, there is a gradually increasing tendency to produce females. In Table VI is a brief indication of this same phenomenon. Males alone (of the sexual individuals) appear in the seventh generation, but a small number of females in the eighth generation. Unfortunately no apterous parents were available for a further generation. If it were possible to obtain wingless females in later generations it would be interesting to note whether they would not eventually produce only females.

Whether there is a similar progressive change in the sexual offspring of winged females is not so clear, since in none of the last three tables of this paper are there any male offspring of alate parents. However, in the

lower half of Table III there is an example of this kind. In the first generation from alate parents there is a minority of males; in the second generation no males. It is not improbable that, if a long line had been bred from alate parents, there would be a progressive decrease in the proportion of male offspring in the sexual phase of the cycle.

3. Tables IV, V, and VI also contain confirmation of the conclusion drawn from the earlier tables, namely, that at any given time winged viviparous parents produce more wingless viviparous offspring than do wingless parents, and that in the sexual phase males are produced chiefly by the wingless parents, sexual females by winged parents.

DISCUSSION

Although the most striking results of the foregoing experiments may appear to be the fact that winged viviparous females produce mostly wingless females in the parthenogenetic part of the cycle and sexual females in the sexual part, whereas the wingless viviparous females produce chiefly winged females in the parthenogenetic phase and males in the sexual, nevertheless the clue to the explanation of this phenomenon is more nearly discoverable in the progressive change in the frequency with which all forms occur in successive generations. Thus, there is a transition from a preponderance of apterous females early in the cycle to a predominance of winged females later. There is likewise, in the sexual portion of the cycle, a transition from males to sexual females. This latter transition has been demonstrated in the offspring of wingless mothers, and is indicated as probable in the offspring of winged females.

These transitions imply a gradual change of some sort, presumably in the metabolism of the animals. While the difference between a male and a sexual female, or between an apterous and an alate viviparous female, may be a definite morphological difference such as a difference in chromosomes, so that an individual is either the one or

the other, not an intermediate, it is hardly possible to escape the conclusion that the thing which brings about or prevents the morphological alteration is a gradual process. What this gradual change may be in the present case can not be known from the evidence, for obviously changes in the type of metabolism may be of various kinds.

Riddle (1917) conceives of such a change of metabolism as a change from individuals having a high rate of metabolism and low energy content to individuals having a low rate of metabolism and high energy content. In the eggs of pigeons forced to lay eggs continuously, he finds just such a change. The early eggs are of the former type, the late eggs of the latter type. From the early eggs are developed males, from the late ones females; and on those facts, supported by other work, Riddle bases an elaboration of the Geddes and Thompson theory of sex.

An attempt has been made to fit the facts obtained from aphids to Riddle's conception of sex. The gradual transition that occurs both in the parthenogenetic and in the sexual phase of the cycle of *Macrosiphum* indicates that one type of metabolism is prevalent early in the cycle, and the contrasted t[illegible]e late in the cycle. The fact that in this transition males precede sexual females shows that, if Riddle's hypothesis holds for the aphids, the progressive change is from a high rate of metabolism and low energy content to a low rate of metabolism and high energy content. Now it has been shown that wingless viviparous females precede winged ones, the change from the one form to the other taking place in part simultaneously with the transition from males to sexual females. Hence in accordance with Riddle's scheme wingless females should represent a high rate of metabolism and low energy content, while the winged ones should possess a low rate of metabolism and high energy content. With regard to the rate of metabolism alone, this assumption is supported by the fact that winged females require longer

to develop, that they produce fewer young per day, and that these young are on the average smaller than in the case of wingless females.

There are certain objections, however, to the foregoing conclusion. First, if winged viviparous females have a low metabolic rate while the wingless ones have a high rate, during the parthenogenetic portion of the cycle a parent with high rate of metabolism produces chiefly offspring with a low rate of metabolism, and *vice versa;* for wingless females produce chiefly winged ones, and winged females produce chiefly wingless ones. On the other hand, in the sexual part of the cycle, parent and offspring are both of the same metabolic type; for winged females (with low rate of metabolism) produce mostly sexual females (which in accordance with Riddle's view should possess a low rate of metabolism), whereas wingless females (high rate) produce mostly males (high rate). Why parent and offspring should be of a similar type of metabolism in the sexual phase, but of unlike type in the parthenogenetic phase, is not clear.

Unless the withholding of food increases the rate of metabolism, or unless the rate of metabolism is taken to mean not the absolute rate, but the rate relative to the food consumed, another objection to the assumption that the winged female possesses a lower rate of metabolism than the wingless ones is found in the work of Miss Gregory (1917). Miss Gregory finds that in *Microsiphum destructor* starvation of the apterous mothers results in the production of more winged offspring. It is only by assuming that starvation increases the rate of metabolism, or that "rate of metabolism" means the relative rate—rate relative to the amount of food consumed, not relative to the rate in another type of individual—that Miss Gregory's discoveries can be interpreted in support of Riddle's hypothesis; providing, of course, that the winged females have a lower metabolic rate than the wingless females.

If, to avoid either or both of the difficulties just men-

tioned, and notwithstanding the slower development, smaller young and smaller daily output of young of the alate females, these winged individuals be assumed to have a higher rate of metabolism than the wingless ones, other difficulties are encountered. This assumption would have the advantage of allowing parent and offspring to be of opposite metabolic type in both the parthenogenetic and sexual portions of the cycle, instead of being of opposite type in the parthenogenetic phase and of like type in the sexual phase. The transitions, however, would be in opposite directions in different parts of the cycle. In the parthenogenetic portion there would be a transition from a low rate of metabolism to a high rate (wingless to winged); while in the sexual part of the cycle the transition would be from high rate to low rate (male to sexual female). These opposite transitions would have to occur in part simultaneously, as in Table IV, fourth and fifth generations.

Unfortunately there has been no opportunity to determine experimentally the rate of metabolism in the various kinds of individuals in *Macrosiphum;* that is part of the program for the future. In the meantime, whether there is a fallacy in the foregoing argument, or a fallacy in Riddle's conception of the relation of metabolism to sex, can not be asserted with any degree of confidence.

Obviously the mere rate is not the only feature of metabolism that may conceivably be related to sex. If there are qualitative differences in the reactions that constitute metabolism, it seems to me more likely that these would influence the development of sexual organs than that the production of ovaries rather than testes could be determined by rate of metabolism alone. Qualitative differences in the reactions might entail differences in the rate of CO_2 production, and therefore be interpreted as quantitative differences. An increase in the output of lumber from a sawmill might be taken to indicate that the saws were running faster than formerly, whereas in reality the saws had been replaced by a new type of saw.

So long as rate of metabolism can be determined experimentally, while the precise reactions can not, there is every reason to continue the attempt to relate the rate of reaction to the course of development. But when facts come to light which do not easily fit preconceived ideas, it is highly important that alternate possibilities be kept in mind.

It is not impossible that the difficulties discussed above may be removed by discovering that the metabolic change that causes the transition from wingless to winged females is different from the change that causes the transition from males to sexual females. The two changes may be more or less independent of each other. In that case it may be possible to separate them experimentally. An agent may sometimes be found which will hasten or postpone the sexual reproduction without in any way affecting the transition from wingless to winged females in the parthenogenetic phase. If this agent hastened the sexual reproduction, it should act as a male-producing factor, since sexual forms would be introduced while wingless parthenogenetic females were more abundant. If, on the other hand, the agent delayed sexual reproduction, it should favor females, since the parthenogenetic mothers would then be more largely winged.

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ORGANIC EVOLUTION AND THE SIGNIFICANCE OF SOME NEW EVIDENCE BEARING ON THE PROBLEM

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I

THE biological problem recognized as having the greatest fundamental importance at the present period is that problem of evolution relating to the means by which the heritable characters differentiating various organisms from one another were first called into existence, or granting the validity of the gene hypothesis and speaking more concisely, how hereditary character-forming genes have originated in the process of evolution. That the diverse forms of life found upon the earth are only to be explained as the result of organic evolution, is a proposition which scarcely needs be mentioned at the present period in the history of science, at least so far as individuals endowed with minds reasonably logical in evaluating evidence are concerned. It is not evolution as a process going on in the world which is being particularly questioned nor the general method by which characters once having originated are inherited, but the particular method by which heritable characters first arose.

The purpose of the essay here presented is threefold. *First,* that of pointing out the unsatisfactory nature of much of the earlier evidence as a basis for sound generalizations in connection with a clear understanding of evolution. *Second,* that of calling attention to the serious shortcomings of modern methodology in throwing light on the causative factors of evolution. *Third,* that of presenting some new evidence somewhat unique in its nature, based in part on preliminary experimental work, to

the effect that the environment acting through long intervals of time may impress characters upon an organism which become unalterable by reversal processes.

To these propositions may be added the suggestion of the fundamental importance which physico-chemical methods must play during the future in solving the problems of evolution.

II

The controversies relating to evolution have been many. When, however, one considers the interest attached to the subject, its broad bearing on various phases of human welfare—sociology and economics in general, animal and plant breeding in particular—together with the difficulties of interpretation which apparently have increased rather than diminished during the sixty or more years seriously devoted to its elucidation, it is not at all surprising that many different conclusions have been reached, many dogmatic statements presented, and many acrimonious discussions engendered.

In connection with a clearer understanding of the points at issue, it will be well to pass certain historical details relating to the development of the different theories somewhat critically in review. This is done even at the risk of a repetition of facts quite familiar to those who have taken more than a passing interest in the subject.

For long the theory of natural selection dependent on the inheritance of small chance variations received general acceptance. Championed by Weismann in his notable controversy with Spencer to the exclusion of the Lamarckian idea that characters acquired through environmental stimuli were heritable, it seemed at the time entirely plausible as an explanation meeting the conditions.

With the greater attention given to experimental methods, however, doubt arose concerning the fundamental value of selection and resulted in the presentation of the mutation theory by DeVries. Here evolution was inter-

preted as arising from sudden and comparatively extreme variations passed on by inheritance in nearly an unchanged condition. Once more the results of experimental work along the lines of the rediscovered principle of Mendelian segregation indicated to a large number of students of evolution that the facts set forth by DeVries were subject to quite another explanation, in itself having no bearing on the origin, but merely on the redistribution of the character-forming units already present in the stock utilized. Another explanation not taking into account the purity or impurity of the parental stock, accounted for "mutations" through the sudden ineffectiveness or loss of a gene.

The dissatisfaction thus arising resulted in the return of many to the fold of "acquired characters." Semon (1912) reviving the "mneme" principle received the support of Wettstein, Przibram, and others. A disinclination existed, however, among most naturalists to accept the evidence presented as seriously upholding the inheritance of new characters produced by environmental stimuli. Explanations of the results on quite other grounds seemed more plausible. For example, the work of Tower (1906), (1910), etc., in attempting to control the color pattern of the potato beetle by changes in temperature and humidity, encountered the impurity of the germplasm objection as well as the gene loss objection, either one of which would be fatal to the validity of the conclusions, if sustained. Commenced at a period in 1895, prior to the rediscovery of the principles dealing with alternative inheritance, and finished in 1904 before the facts were duly appreciated, it is not at all improbable that genetic complications in the way of recessives, modifiers, losses, lethals, etc., were involved. The destructive criticism presented by Cockerell, Gortner, Bateson, Castle, and others, particularly in reference to the later studies of Tower (1910), makes it evident that the results must be confirmed from independent sources with more consideration to the possible errors mentioned before the conclusions are to be accepted.

Similarly, the work of MacDougal (1907), in connection with the modification of *Raimannia odorata,* one of the Patagonian primroses, may be explained. Compton, as noted by Bateson (1912), using the same species, was unable to obtain like results, while Humbert (1911) utilizing 7,500 pure line plants of *Silene noctiflora,* one of the "pinks" also failed to obtain so-called "mutants" similar to those found by MacDougal.

The investigations of Kammerer, Woltereck, Ferroniere, etc., are of decided interest, but to those critically inclined they offer no evidence giving pronounced support to the proposition that environmental stimuli form new genetic factors.

Thus, in turn, have the theories as to the method by which evolutionary progress occurs been undermined by doubt. Feeling the insufficiency of small chance variations, of environmental variations, and of larger germinal variations, as a summation process, it is not to be wondered that the truth-seeking pilgrim has become wearied in his journey and longs for a more secure resting place.

III

Let us return to the problem as suggested in the opening paragraph, namely the actual origin of heritable characters, and consider somewhat more carefully as to whether theories exist justified by facts, which will furnish acceptable evidence. There are two well-developed hypotheses, the general one of DeVries and the more specific one of Morgan and his associates, founded on discontinuous variations, and that of Castle based on continuous variations.

Considering the views of DeVries and his followers in the light of experimental investigations made during the last ten years, it has become more and more evident that by far the greater number, if not all, of the so-called mutations thus obtained, were explainable on the basis of the combinations of preexisting units of the germ cells. This rests upon the proposition that there are present in the

gametes certain hypothetical entities to which the name gene or factor has been applied and which give rise to the heritable characters of an organism. Thus it is at once recognized that the problem relates to the origin of the gene, rather than to the origin of the apparent characters with which it is correlated, and that by far the greater number of so-called new characters are not new, but were performed at remote periods of time. So far as the present arguments are concerned, it matters not whether the results are assumed to be brought about by material units or enzyme reactions. The prepared potentialities exist in either case.

As examples of extreme types of characters which may arise from the combinations of existing genes and which might have been considered "mutations" at an earlier period when the facts as to their origin were not fully known, one need only mention the "blue" of the Andalusian Fowl exhibited by the hybrid between the black and white parental stock, or the "pink" presented by the cross between the red and white "four-o-clocks" of Correns. A type of characters more in line with mutations which have been described and to which there is every reason for believing that many of them may be referred, rests upon multiple gene effects combined with sterility, in accordance with evidence presented by Davis, and others. Of decided interest in this connection is a recent paper by Muller (1917) calling attention to "An *Œnothera*-like case in *Drosophila*" where a result quite comparable to certain mutations of *Œnothera* is explained through the action of balanced lethal genes. There are other varying degrees of combinations from which "mutant" characters may arise and which depend on the behavior of the genetic material in connection with recessives, modifiers, lethals, crossovers, non-disjunction, etc.

There is really nothing extraordinary in the appearance and disappearance of the characters thus formed, beyond their interpretation, and this has furnished false premises for many erroneous conclusions, chief of which,

in the opinion of the writer, is the mutation theory as outlined by DeVries in so far as it may account for progressive evolution.

Inasmuch as it seems probable that the results obtained by Castle are to be explained upon the same basis as those of DeVries, it will be well to consider them in this connection. Here it is assumed that a continuously variable heritable gene is involved, and that progressive results are obtained through the selection of the "unit characters" produced by such a gene. Castle, however, stands almost alone in vigorous support of such a variation, while opposed to him are the Hagedoorns, Morgan, Pearl, Punnett, McDowell, Muller and others equally insistent that genes once having originated pass on from one generation to another unchanged except in comparatively rare instances where so-called "mutations" occur.[1] It is maintained by those advocating this view that the results in connection with hooded rats on which Castle bases his contentions, are due to an uncertain number of modifying genes not in themselves variable, and that the existence of such genes has been demonstrated in other organisms presenting results similar to those obtained in rats. The work of Little (1917) with mice where three segregating types of spotting were found to produce varying degrees of color pattern, indicates that multiple genes are involved. Furthermore, the analysis by Little of the data obtained by Castle, Phillips and Wright, points decidedly to the interpretation of their

[1] Jennings (1917) has recently endeavored to show that the views of Castle and his opponents are identical. This, however, is by no means the case. On the one hand there is the idea of a continually variable gene (coat-color-producing gene in rats) moved gradually along a given scale by selection. On the other hand there is the idea of a rarely mutating gene (*e. g.*, sex-limited eye color producing gene in *Drosophila*) moving abruptly from one part to another of the scale. Its position once obtained remains for a long time constant. These differences of interpretation are at present irreconcilable.

Since this note was written, Morgan (1917) has discussed the matter in detail, presenting arguments quite similar to those mentioned above, and arriving at a similar conclusion.

results on the basis of multiple genes instead of a continually varying gene.

It would thus appear evident that the theory outlined by Castle is open to quite the same objections that occur in connection with the mutation theory of DeVries, and that there is little evidence for believing that it has any fundamental value in explaining evolution.

The mutation theory of Morgan and his associates, based primarily on results obtained in studies of the small "fruit-fly" *Drosophila,* apparently presents quite another view of the subject. Here it is clearly indicated that evolution has taken place through the incorporation of mutant changes, and that these changes are due to discontinuous "mutations" of genes as exemplified in multiple allelomorphs.

Assuming the validity of the arguments based on linkage relations in respect to the localization of the genes, the conclusion follows that the "mutation" results either (1) from a change in a specific gene or (2) from the complete linkage of a series of genes. If the latter proposition should be the correct interpretation, and it is by no means clear that it is not, the objections urged against the theories of DeVries and of Castle hold equally here.

Morgan and several others have presented evidence for believing in the specific change of a gene. Granting that this is the actual explanation of the facts presented in connection with multiple allelomorphs, etc., there are two lines of argument leading to the conclusion that these changes are results of combinational sub-units or subgenes existing in the species, and that progressive evolutionary changes are no more represented here than in the previous theories of DeVries and of Castle.

The first argument (*a*) rests upon the recurrent "mutations" which have been noted in a considerable number of cases. Thus the sex-linked eye colors of *Drosophila* forming the multiple allelomorph system consisting of white, eosin, cherry, blood, tinged, and buff, and their dominant allelomorph, red, of the wild fly, have their

origin from a single definite area or locus in the "X" chromosome, accepting linkage as a criterion. They have not arisen in a continuous series but as sudden changes from one extreme to another at comparatively long intervals. The character may remain modified in one direction and then suddenly revert to an original condition. Thus white changed to eosin and later back to white as noted by Morgan (1916). Furthermore, the changes are not extremely infrequent. A similar transformation has been noted by Emerson (1917) in maize where self color apparently changed to variegation and later back to self color. A variation which may be of the same type has been described by Shull (1911) for *Lychnis*. Quite recently Zeleny (1917) in studies on *Drosophila melanogaster* Meig. (=*ampelophila* Löw)[2] has noted a reversed mutation where full-eyed flies result from the return of the bar gene to the original full-eyed condition. In each of the cases mentioned the germinal purity of the stock was believed to be without question.

Such results are not to be attributed to a continuous series of mutations, to progressive changes, or to genetic losses. They clearly suggest that the gene, if it is the individual gene which is involved, is made up of smaller combinational units which through their permutations give rise to the characters in question. Presumptive evidence is certainly furnished against the idea that anything new has developed in the organism to form the particular characters. Furthermore, one may well believe that any particular mutation under observation sufficiently long, will exhibit recurrent changes.

The second argument (*b*), to the effect that the gene is comparatively stable and that "mutations" are only transitory combinational changes, is based on the maintenance of apparently identical genes through long periods of time. Thus Metz (1917) found that the three mutations which had, up to that time, occurred in *Drosophila virilis* Sturt. appeared exact duplications of the

[2] Sturtevant, mss.

mutations in *Drosophila melanogaster* Meig.[3] In both species "confluent," a modification of the wing venation, is similar in form, dominant over "normal" and "lethal," when the fly is homozygous for the character. The characters "yellow" and "forked" are sex linked in both species and otherwise alike so far as the evidence exists. Inasmuch as the earliest representative of *Drosophila* thus far known is a species not decidedly different from those now existing as noted by Löw (1850), who described it from the amber of the Baltic Sea, and belongs to the Lower Oligocene of the Tertiary Period, with an age of from two millions to three millions of years, one must infer that the genes common to the two species mentioned have been preformed for a long period of time, and that nature has paid little attention to such mutational changes as occur in connection with multiple allelomorphs.

There are certain investigations widely separated as to their content, but apparently closely correlated as to the underlying explanatory principles involved, which must not be overlooked in a consideration of the changes which may take place in hereditary units. These are concerned with the differences involved in metabolism.[4]

On the one hand there are studies dealing with the direct effects of a changed metabolism on the developing individual. Here may be mentioned the work of Lillie in connection with the "free-martin" of cattle; Steinach on the transplantation of the gonads in rats and guinea-pigs; Goodale on the grafting of ovaries in male fowls; Pearl and Surface on the degeneration of the ovary in cattle; Riddle with pigeons, etc. On the other hand, there are studies dealing with the indirect effects on inheri-

[3] The species are distinctly separated not only in external appearance but also by their chromosome number. *D. melanogaster* has four pairs, while *D. virilis* has five pairs of chromosomes.

[4] The theory has had a long historical development. Treat (1873) published a paper on controlling sex in butterflies as a result of food supply. Yung (1881) worked with tadpoles. Nussbaum (1897) with rotifers. Recent evidence of an elaborate nature has been presented by Goldschmidt, Woltereck, Whitney, Banta, Shull and others.

tance. Among these may be mentioned that of Goldschmidt with moths; Woltereck with daphnids; Plough with temperature effects on *Drosophila*; Hoge with the effects of cold on *Drosophila*; Morgan with the effects of moist food supply on *Drosophila,* etc.

As an example of the development group, the investigation of Lillie may be noted. The evidence obtained showed that the "free-martin" or sterile female usually developing where the twins are of separate sexes in cattle, etc., resulted from the modifying influences of the sex hormones in the male where the two chorions had anastomosed.

As an example of the inheritance group, Morgan has found that the "mutant" "abnormal abdomen" in *Drosophila* occurs in connection with a moist food supply. The character is a sex-linked dominant. If an abnormal male is bred to a normal female and the food is kept moist, the sons are normal and the daughters abnormal. If the food is dry both sons and daughters are normal. The reciprocal cross gives sons and daughters both abnormal with moist food but normal with dry food.

It follows then that in *Drosophila* the gene for the abnormality—or the chemical preparedness for the inhibition of normality, if one so wishes to term it—is performed in the "X" chromosome and merely awaits a suitable environment before presenting itself as a character. Similarly, in connection with the changes occurring in the development of the "free-martin" of cattle, it seems necessary to admit that there are genes present in the sex chromosome concerned with the development of sexual characters which, however, are in a state of equilibrium, and that the inhibition or the excitation[5] of one or the other genes or groups of genes will result in the development of the corresponding individual.

From the facts presented, one seems justified in making the deduction that heredity hands down a framework

[5] It has been shown by Chapin (1917) that the gonads of the free-martin originally destined to be a female, attain a male condition.

which within certain limits allows a plasticity in the development, and that the direction of development is determined by physico-chemical influences through the suppression of potential units.

Thus the conclusion seems almost unavoidable that by far the larger number, if not all, of the heritable characters making up an organism, result from combinational units which have long been predetermined, and that the breeder, whether the semi-scientific agriculturist or the ultra-scientific drosophilist, is largely, if not entirely, engaged in presenting new combinations of existing units. If this be true, modern genetics has left the actual problem of evolution far to one side and deals only with results of a secondary, although none the less interesting, nature.

One is, therefore, led to inquire as to whether there may be available evidence which will permit a new insight into conditions governing the formation of characters, even though the evidence from its nature must be largely circumstantial.

IV

Accompanying the progressive swimming movement of most aquatic microorganisms there is a characteristic axial rotation. This has been noted by Nägeli, Engelmann, Strassburger, Mast and more in detail by Jennings (1901) who has called attention to the value which such a compensatory motion may have for the organism in which it exists. No explanation has been suggested other than this as to the origin of the rotation, and without further thought it is evident that one would be inclined to attribute it to natural selection, assuming that those individuals in which it did not occur were at a disadvantage in the struggle for existence by reason of their more confined movement.

It is the phase of the question dealing with the particular causes bringing about the rotation that appears to be of extreme significance when considered in connection with the principles underlying evolution and to be

susceptible to quite another explanation than the natural selection implied by the term "adaptiveness" which, in accordance with Jennings (1906), is based on the idea that "it tends to preserve the life of the animal." Furthermore, when the groups of facts associated with the characteristic rotation are brought in review, it would seem that the explanation suggested may go far toward interpreting the origin of the fundamental activities as well as the origin of the characters in general of organisms.

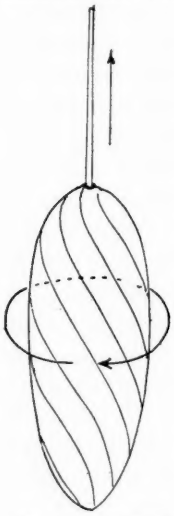


FIG. 1. Typical Euglenoid Flagellate illustrating left-hand spiral arrangement of striæ in connection with clockwise rotation (observer in front) and progressive movement by means of anterior flagellum.

In connection with the preparation of a systematic review of the order Euglenoidina belonging to the class Flagellata of the Protozoa (1915), it was noted with decided interest that a large number of the forms possessed an oblique striation ranging from almost indiscernible markings to characters of great complexity impressed upon a cellulose-like envelope (*e. g., Euglena spirogyra* Ehrenb., *Phacus pyrum* (Ehrenb.), *Heteronema spirale* Klebs, etc.), the striæ extending forward and to the left. The character also appeared to be invariably correlated with an axial rotation of the organism from right over to left (Fig. 1). Such a movement is to be described in physical terms as "clockwise," the position of the observer being in front of the advancing organism.

The facts took on additional interest when it was noted that forms with a reverse striation seemed entirely absent from the northern hemisphere, although such forms existed in the southern hemisphere.

Inasmuch as the euglenoids are in general positively phototactic under normal conditions, it would immediately occur to one seriously considering the question, that

the underlying principle producing the rotation was the turning of the earth on its axis, with the resultant apparent motion of the sun from east to west. Such a hypothesis would become the more tenable when it was found that negatively phototactic microorganisms of the northern hemisphere rotated as a rule in a reverse or counter-clockwise direction.

Some of the evidence thus far obtained may be presented more clearly in tabular form[6] (Table I). Thus

TABLE I

A series of aquatic microorganisms showing in general the clockwise rotation of positively phototactic forms and the counter-clockwise rotation of negatively phototactic forms in the northern hemisphere, with evidence for the tendency to reverse condition in the southern hemisphere.

Northern Hemisphere		
Euglena viridis Ehr.	Positive.	Clockwise.
Euglena hæmogranulata Walt.	Positive.	Clockwise.
Euglena tripteris Duj.	Positive.	Clockwise.
Euglena spirogyra Ehr.	Positive.	Clockwise.
Leptocinclis ovum (Ehr.)	Positive.	Clockwise.
Phacus pyrum (Ehr.)	Positive.	Clockwise.
Cryptomonas ovata Ehr.	Positive.	Clockwise.
Pandorina morum (Müll.)	Positive.	Clockwise.
Eudorina elegans (Ehr.)	Positive.	Clockwise.
Volvox globator (Linn.)	Positive.	Clockwise.
Stentor polymorphus Ehr. (= *viridis*)	Positive.	Counterclockwise.
Phacus longicauda Ehr.	Positive.	Counterclockwise.
Stentor cærulus Ehr.	Negative.	Counterclockwise.
Anurea cochlearis Gosse	Negative.	Counterclockwise.
Arenicola cristata (larva)	Negative.	Counterclockwise.
Chilomonas paramœcium Ehr.[1]	Negative.	Counterclockwise.
Southern Hemisphere		
Leptocinclis piriformis Cun.	Positive?	Counterclockwise.
Phacus bacillifer Cun.	Positive?	Counterclockwise.
Leptocinclis mammilata Cun.	Positive?	Clockwise.

it may be stated that so far as the facts are available, positively phototactic forms with the exception of

[6] The rotation direction and light responses noted are those taking place under normal conditions. The conclusions presented are not altered by the fact that as a result of stimuli under conditions imperfectly known, reverse movements may occur, *e. g.*, the negative response of Euglenoids to intense light.

Stentor polymorphus Ehrenb. (=*S. viridis* aut.) and *Phacus longicauda* Ehrenb. rotate clockwise in the northern hemisphere. Inasmuch as the phototactic relation of the ciliates in general is negative, where a reaction exists, it seems probable that the inclusion of the minute symbiotic forms of algæ, *Chlorella vulgaris* Beyer, which gives the species its characteristic green apperance, has induced a change from a negatively phototactic to a positively phototactic condition, while the organism retained its original counterclockwise rotation. Small forms like *Chlorella* which contain chloroplasts, are generally positively phototactic so far as their responses to normal conditions are known.

Phacus longicauda (Ehrenb.) is an euglenoid about 100 μ in length, with comparatively flat wing-like expansions. The striæ covering the body are longitudinal. In swimming, however, many of the forms have the anterior part of the right expansion turned slightly down, while the left expansion is turned up in a similar manner. This gives their progressive movement a counterclockwise rotation.

In the southern hemisphere direct observation of the characteristic rotation has not been made, but inasmuch as the direction of the striæ indicates the direction of the rotation, certain evidence is available. Cunha (1913) in his studies of Protozoa from Brazil has figured several forms showing distinctly the arrangement of the striæ in the excellent plates drawn by himself. While it is not impossible that a careless investigator might focus on the lower part of the specimen, thus showing the reverse position of the striæ, the careful work of Cunha scarcely permits one to suggest such a criticism. It may furthermore be noted that the apparently counterclockwise rotating forms described by him are species quite different from the typical northern forms, while the forms which evidently rotate clockwise are closely allied to species from the northern hemisphere, and may have been introduced comparatively recently so far as evolutionary time is concerned.

The original development of the unicellular forms in the northern hemisphere with their subsequent introduction to the southern hemisphere by aquatic birds, etc., is well within the range of possibility and suggests that even should forms with reverse rotations be entirely absent from south of the equator, the hypothesis which has been proposed would by no means be invalidated.

Having presented the general facts as to the behavior of free-swimming microorganisms, it becomes advisable to consider the explanations which may exist as to the origin of the characteristic rotation. It seems impossible to attempt to account for such a character on the ground of "natural selection." One would be compelled to believe that the reverse rotation—the counterclockwise rotation of positive northern forms—possessed an elimination value, an almost indefensible proposition, particularly when forms like *Stentor polymorphus* and *Phacus longicauda* are considered as well as forms in the southern hemisphere which do not rotate in agreement with theory.

The most obvious explanation to be considered is that based on the influence which the sun in its apparent daily movement from east to west in the equatorial region may be supposed to have exerted on the flagellum (Fig. 2). This assumes that the flagellum is the orienting factor and that the sun has induced in it an east-west rotary-like or whip-like propelling movement. The consequent mechanical effect would be that in the northern hemisphere forms with a positive light reaction would rotate clockwise and those with a negative light reaction would rotate counterclockwise. Conditions would be reversed for those which might be present in the southern hemisphere during the evolutionary stage.

Conversely, negatively phototactic forms would develop a reversed or counterclockwise rotation by means of the influence of the light rays on the stroke of the light avoiding flagellum and their modified organs, the cilia. It is by no means necessary to believe that the stroke of

the flagellum should be one of rotation, although theory would imply a partial rotation in the primitive flagellate forms. The method of movement by means of the flagellum furnishes a problem of considerable difficulty which

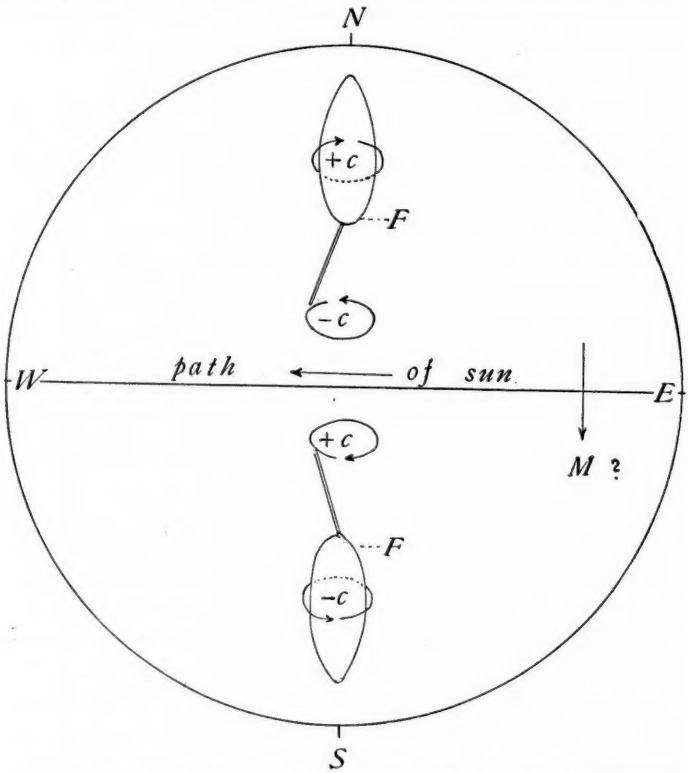


FIG. 2. Illustrating the theory as to the origin of axial rotation in aquatic microorganisms of the northern and southern hemisphere of the earth by the apparent movement of the sun from east to west. *N*, etc., north, etc.; *F*, flagellate organism; $+c$, $-c$, clockwise and counterclockwise rotation of organism (observer in front); $+c'$, $-c'$, induced clockwise and counterclockwise movement of flagellum; *M* ?, possible southern migration of forms which have retained primitive rotation.

has received attention from several investigators, notably Delage and Herouard (1896), Goodspeed and Moore (1911), Bütschli and others.

There are several inferences of an axiomatic nature

that follow from such an hypothesis. Forms near the neutral equatorial region may be assumed to possess a slower rotation than forms near the poles and at the same time there may be expected to occur a change in the relative angle which the striæ make with the longitudinal axis of the body, their direction becoming approximately parallel with that axis. The cosmopolitan distribution of unicellular organisms with the evident non-selective value of the character makes such a hypothesis difficult of demonstration. The application of statistical methods would be of interest, however.

A second explanation of the rotation direction, apparently, however, a negligible one, is on the basis of the angular velocity of the earth so far as it may have an influence on small bodies at its surface. With free-swimming microorganisms oriented in accordance with the axis of the earth during definite intervals and rotating in the same direction that the earth rotates, conditions are fulfilled for such a mechanical explanation. When, however, the relative dimensions of the earth and the organisms as well as the relative density of the earth, the water and the organism, are considered, it is difficult to believe that the explanation lies in this direction. While many of the forms are attached to some definite surface in the water during certain periods of their development, there are others which reproduce directly in the water and should this have been the primitive condition of development, the rotation of the earth would have been ineffective.

While the possibility of electrical forces may be mentioned as an influence, there are no facts known which allow an interpretation in this direction.

During the past two years a considerable number of experiments have been made in attempts to obtain some definite evidence as to the cause of the rotation. Obviously it would be of interest to maintain a culture of northern forms in the southern hemisphere or a culture of southern forms in the northern hemisphere. Efforts

to obtain living cultures from desirable localities, the Falkland Islands, New South Wales, the southern part of South America, etc., have thus far failed. A method, however, was devised by which it seemed theoretically possible to subject northern flagellates to an environment similar to that of the southern hemisphere. A clinostat (Fig. 3) having a clockwise rotation of fifteen minutes

FIG. 3. A clinostat arranged for the purpose of subjecting northern flagellates, etc., to an apparent west-east movement of the sun, the covered portion being toward the north.

was procured, a circular table ten inches in diameter fitted to this, and the northern half covered so that the revolving table containing slides in excavated recesses would pass into darkness on one side and emerge moving from east to west. Thus the apparent path of the sun so far as the organisms were concerned would be from west to east. The larger unstriated *Euglena* have been used almost entirely in the experiments, inasmuch as it would apparently be impossible to change the direction of rotation in forms like *Euglena spirogyra* Ehrenb., *Phacus pyrum* (Ehrenb.), etc., where the striæ are carinate in structure with an angle almost if not entirely precluding a rotation in the direction opposite to that in which they were accustomed to turn.

FIG. 4. Flagellate forms from the northern hemisphere illustrating the development of the left-hand strip. *A*, *Euglena hemogranulata* Walton (Ohio); *B*, *Euglena spirogyra* Ehrb. (Ohio); *C*, *Urceolus costatus* Lemm. (Europe); *D*, *Heteronema spirale* Klebs (Europe).

While there has been a large amount of data obtained, thus far no evidence shows that either a "reversal" or a "slowing up" of the rotation may be produced in any of the individuals utilized.

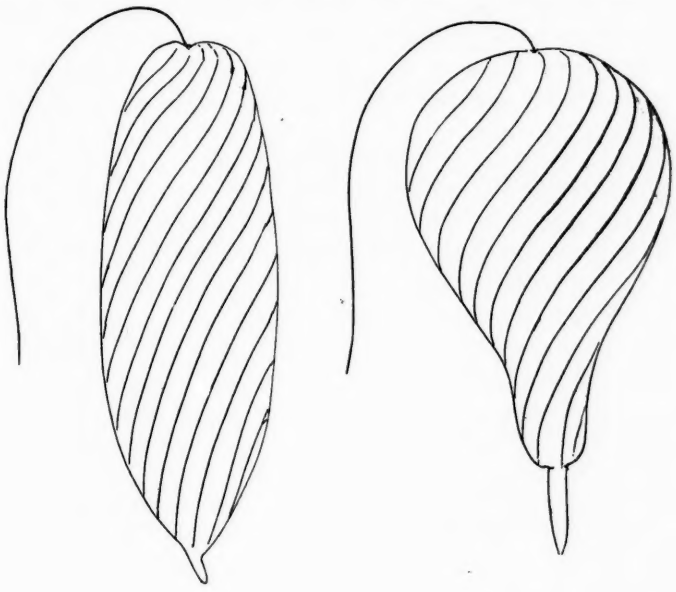
Even though it may not be possible to change the direction or the period of rotation in "adult" forms, may not such changes be produced in encysted forms or during a period when gametes are developed. Experiments are yet to be made with individuals in an encysted condition, and with material available it will be possible to utilize gamete-producing forms. That *Euglena* has a sexual cycle was pointed out by the writer nearly ten years ago (Walton, 1909).[7] Certain forms encyst, the cysts subdividing to approximately a 16-cell stage, small flagellate gametes emerge and conjugate. An experiment of this nature involves a discussion of the environmental effect on germ cells as compared with somatic cells, but does not affect the issues with which we are concerned in the present paper.

There are many other questions of interest which arise in a study such as outlined. For instance, what has been the origin of the striæ which are much specialized in many forms, although entirely absent in other forms (Fig. 4) so far as visibility with the microscope is concerned. The majority of the positive northern forms have "left-handed" striæ, a smaller number have longitudinal striæ, while a considerable number appear to have no striæ. None have been found with "right-handed" striæ. At first one may be inclined to attribute such a character to natural selection, but when one commences to ascertain the value of the character on the basis of progression, rotation and axial angle, such a conclusion seems less certain. There are a few facts that appear evident. First that the development of the striæ has been at a considerably later period than that of the rotation direction. Second that the relative position of the striæ has been largely dependent on the rotation. Third,

[7] Paper presented at annual meeting of Ohio Academy of Science, 1908.

that the development of the striæ has in many forms proceeded so far that a reversal rotation seems an impossibility.

The presence of a considerable number of other groups which have "left-handed" spirals so far as observation goes, is of interest. The various genera of Spirochætes, as well as *Spirulina* and *Arthrospira* among the *Cyano-*



A *B*

FIG. 5. Flagellate forms from the southern hemisphere, Rio de Janeiro, Brazil (from Cunha), illustrating the development of the right-hand striæ. *A, Phacus bacilifer* Cunha; *B, Leptocinclis piriformis* Cunha.

phycoidea (*Cyanophyceæ*) may be mentioned. The twining of plants may, in the final analysis, be attributable to the same cause.

Other related problems are the pendulation theory of Simroth (1912) relative to bipolar distribution, and the tropism theory as outlined by Verworn (1894), in connection with the excitation contraction of the flagellum.

V

Having indicated some of the difficulties existing along the lines of established research in the efforts to account for the derivation of the fundamental heritable units making up an organism and having presented a series of observations suggesting that a new perspective may be obtained by utilizing methods of attacking the problem somewhat different from those hitherto employed, the particular purpose of the paper is accomplished.

It may be asserted by some that such an attempt at a summary disposal of the existing evidence as to the actual origin of characters represents an unfortunate type of destructive criticism. Furthermore, that the acceptance of the validity of the arguments as to the long predetermined nature of the genes or subgenes, leads us once more in the direction of the somewhat antiquated theory of preformation. It is not impossible that these views are in part justified. Nevertheless it is well within the bounds of propriety to occasionally inquire as to whether the enthusiasm developed for a special discovery has not resulted in too broad an application of its principles. The mutation theory particularly as developed by Morgan is of interest. It is circumscribed at least in part by the phenomena of mendelian inheritance, and it is evident that one should look farther for the facts which may assist in explaining the real origin of the diversity of living things.

If additional studies support the view suggested by the facts here presented, namely, that characters of a physiological nature may be produced by environmental causes, and that these in turn may demand the correlation of morphological characters regardless of the origin of the latter, an important step will have been made in accounting for the primary differentiation of organisms. The later secondary differentiation through the combinations of units which have thus arisen, and which attains its maximum in the complex multicellular animals and plants, offers no particular difficulties in its explanation.

Furthermore, such an idea is more in harmony with the paleontological evidence as presented by Osborn (1912) and others, than one based on the mutational idea, and it is to fossil forms that one must look for the all-important historical record.

Should one propose a hypothesis of an ultimate unit, slightly plastic as to its immediate environment, but subject to the permutations and combinations of a mendelian type, and possessing a definite qualitative condition determined by prolonged environmental action, the picture is not at all so fanciful as some might at first thought insist.

The practical importance of such a viewpoint in its application to the problems of animal and plant breeding lies in the realization that new forms can not be created, but merely new combinations uncovered during the comparatively brief epochs of time which human intelligence has for working out the processes. Thus one returns to genetics.

In summarizing the paper, the following conclusions are suggested:

I. The heritable characters in general which make up an organism arise from preformed units in the nature of genes or subgenes that have been in existence during long geological periods of time. There are at present no criteria available in modern genetics by which an apparently new gene may be distinguished from one long in existence; furthermore, there is doubt as to whether new genes are actually arising in multicellular organisms. The change of a gene in a given direction, whether it be considered as a morphological unit or a chemical condition followed by the return to its original condition, suggests its composition of combinational sub-units, and is an argument against the idea that anything actually new has come into being during its series of so-called mutations. Such a conclusion receives additional support from the presence of apparently identical genes which exist in distinct species of organisms separated during

long epochs of time, as well as from the evidence of the non-contamination of genes during diverse environments.

II. The mutations demonstrated by DeVries and others, together with the variations obtained by Castle, are to be interpreted as a result of the combinations of existing genes. The mutations noted by Morgan and his associates, as evidenced from recurrence and stability, are in the nature of modal fluctuations having no definite cumulative value.

III. The direction of axial rotation in aquatic microorganisms is best explainable on the basis of the apparent east-west motion of the sun having influenced the movement of the organs of locomotion. Thus the character becomes one acquired from external stimuli, and the persistence of reverse forms in both the northern and southern hemispheres indicates the hereditary nature of the character. Morphological characters, such as the striæ, etc., may arise in a similar manner or through selection. By correlation with the preceding characters, a cumulative and irreversible effect is produced.

IV. The primary factors in evolution are environmental and thus dynamic. The secondary factors of a combinational nature are gradually approaching a limiting maximum value, and are thus becoming static.

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SHORTER ARTICLES AND DISCUSSION

RHYTHMIC SYNCHRONISM IN THE CHIRPING OF CERTAIN CRICKETS AND LOCUSTS

SYNCHRONISM in the rhythmic chirping of the snowy tree cricket, *Œcanthus niveus* De G., has been observed and mentioned by a number of able observers, including Burroughs, Thoreau, McNeill and Dolbear. The synchronous chirping of this particular cricket has been too generally observed to be considered merely an illusion of the mind. In a previous paper[1] I reported that I had observed the occurrence of rhythmic synchronism in the chirping of colonies of the tiny tree crickets, *Cyrtoxipha columbiana* Caudell in Georgia. During the summer of 1917 I was afforded an excellent opportunity to make further observations of the synchronous chirping of these interesting arboreal crickets near Vinson Station, Virginia. A little colony had become located in the crown of a small black cherry tree in my back yard, where I could readily keep them under observation at all times. During the latter part of August, when the chirping season was at its height, a remarkable degree of synchronic rhythm characterized their chirpings during warm, quiet evenings. So constant was this rhythmic synchronism that only now and then would any irregularity occur. It finally occurred to me that I could subject their consecutive chirpings to a fairly accurate statistical analysis in the following manner. With a tablet of paper and a pencil I made a short horizontal dash for those instances when the chirpings were in unison, and a short vertical dash when they were not in unison. In this way I was able to record the consecutive chirpings for certain periods of time. In order to illustrate this method, I will give a graphic expression of the first period, which included 98 consecutive chirpings, 8 of which were not in unison.

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Fourteen different periods of consecutive chirpings were re-

[1] "Synchronism and Synchronic Rhythm in the Behavior of Certain Creatures," AM. NAT., Vol. 51, July, 1917.

corded in this manner, the results of which may be noted in the following table:

TABLE I

STATISTICAL ANALYSIS OF 14 DIFFERENT PERIODS OF CONSECUTIVE CHIRPINGS OF A COLONY OF CRICEKTS OF THE SPECIES *Cyrtoxipha columbiana*

Period	Consecutive Chirpings Recorded	Chirpings in Unison	Per Cent. of Chirpings in Unison
First	98	90	91.8
Second	79	72	91.1
Third	85	72	84.7
Fourth	23	21	91.3
Fifth	78	72	92.3
Sixth	84	79	94.0
Seventh	66	59	89.3
Eighth	73	69	94.5
Ninth	45	44	97.7
Tenth	23	19	82.6
Eleventh	71	68	95.7
Twelfth	21	21	100.0
Thirteenth	75	74	98.6
Fourteenth	49	48	97.9
Total	870	808	92.8

From these data it would appear that out of a total of 870 chirpings observed, 92.8 per cent. were in unison. Even granting that some errors have been made in these determinations, it is quite evident that this observed high percentage indicates that a remarkable degree of synchronic rhythm occurs.

I kept this particular colony of four or five crickets under observation for a long time, and this rhythmic synchronism was always very noticeable. These crickets chirp most actively just before sundown. At this time every individual chirps briskly, and it is not long until chirping in unison is gradually established. This rhythmic synchronism does not take place at once, but becomes evident after the crickets have been chirping steadily for some time. When this rhythmic unison is fairly established it appears difficult for the crickets to chirp otherwise, for if there is any tendency toward asynchronous chirping, it is quickly overcome. A remarkable feature of the chirping of these crickets is a tendency now and then for the chirping to become noticeably accelerated briefly. Even though this occurs, the entire group keeps pace, so that the same unison is maintained.

The mole cricket (*Gryllotalpa borealis* Burm) is not an uncommon species in low grounds in this part of the country. Its notes

are low, mellow, intermittent chirpings—gur-r-r-r-r, gur-r-r-r-r, gur-r-r-r-r—which may be kept up almost incessantly during the active mating season. I have never been able to observe any definite rhythmic synchronism in the chirping of these burrowing crickets. However, late in August, during the season of 1918, I attempted an analysis of the notes of two of these crickets which were stridulating at the same time in their underground burrows in a wet spot near Vinson Station, Virginia. These two individuals chirped very persistently, and at times I noted some degree of synchronism.

TABLE II

STATISTICAL ANALYSIS OF 10 DIFFERENT PERIODS OF CONSECUTIVE CHIRPINGS OF TWO MOLE CRICKETS, *Gryllotalpa Borealis*

Period	Consecutive Chirpings Recorded	Chirpings in Unison	Chirpings Not in Unison	Per Cent. of Chirpings in Unison
First	46	30	16	65.2
Second	36	18	18	50.0
Third	62	36	26	58.0
Fourth	53	28	25	52.8
Fifth	28	16	12	57.1
Sixth	48	21	27	43.7
Seventh	37	14	23	37.8
Eighth	47	29	18	61.7
Ninth	21	10	11	47.6
Tenth	46	20	26	43.4
Total	424	222	202	52.3

From these data, which indicate that out of a total of 424 chirpings only 222, or 52.3 per cent., were in unison, it would appear that there was no particular tendency to maintain a definite synchronism in their chirpings.

The most remarkable instances of rhythmic synchronism I have ever heard have been afforded by the cone-headed grasshopper of the species *Neoconocephalus exiliscanorus* (Davis). A careful study of the intermittent notes—zeet-zeet-zeet-zeet—of these locusts was made on the edge of a swamp near Vinson Station, Virginia, late in August, 1917.

The characteristic habit of stridulation for individuals of this species is to produce a certain number of consecutive notes, followed by a brief pause. Usually, from fifteen to thirty consecutive notes are delivered before the pause takes place, then stridulation is again resumed. Rehn and Hebard[2] mention this habit as follows:

[2] Rehn, James A. G., and Hebard, Morgan, "Studies in American Tet-

The number of consecutive times without pause that this sound was produced were on one occasion counted, 26–14–20–20–17; usually on a warm evening an undisturbed singer would average about as above before ceasing a few seconds. The song is rapid, the sounds being emitted on warm evenings about 3 to the second.

When stridulation has become fairly established in a colony of these locusts, for the evening, it is likely to be continuous, for if some singers cease their notes briefly, others take up. Rehn and Hebard, in the publication mentioned above, have also noted this behavior and say:

When near a colony of this species on favorable evenings after dark the air is vibrant with the sound; as several singers cease others take up the constantly rising and falling song, but at no very great distance the song is inaudible.

In the colony observed by the writer at Vinson Station, Va., three individuals which were somewhat isolated from the rest maintained a perfect rhythmic synchronism for many minutes at a time, including in this period many hundreds of consecutive notes. Now and then all three would be stridulating at the same time, then only two would produce their notes, yet the same perfect rhythmic synchronism was always evident. Sometimes all but one would cease to stridulate, then one or both of the others would again take up the rhythm with a precision that was marvelous. It did not matter how often one or another individual joined the chorus following a pause, the notes were always perfectly synchronous from the start and the rhythmic synchronism was maintained.

A representation of this perfect synchronism which was evident as the different "singers" took up the rhythm from time to time may be shown graphically with dashes as follows:

On several different nights I observed the same marvelous rhythmic synchronism in this particular group of individuals. Although other groups were "singing" elsewhere, it appeared

tigoniidæ: A Synopsis of the Species of the Genus *Neoconocephalus* found in North America, North of Mexico," in *Trans. Ent. Soc.*, 40, Jan. 6, 1915, pp. 365–413.

that their notes were delivered independently of the rhythm of this particular group. From observations of the stridulations of other groups in this same colony, I am of the opinion that it is not unusual for these locusts to develop a rhythmic synchronism in small groups.

It would be interesting to know why some species of locusts and crickets possessing the intermittent habit of stridulation tend to develop a more or less perfect rhythmic synchronism while others do not. Although this is true of the two crickets, *Œcanthus niveus* and *Cyrtoxipha columbiana*, I have been unable to note any synchronism in the chirpings of the common arboreal cricket, *Orocharis saltator*. Although large colonies of these crickets may often be heard in stridulation, each individual appears to stridulate in its own leisurely manner independently of its fellows.

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ON THE PIGMENTATION OF A CLYPEASTROID, MELLITA SESQUIPERFORATUS LESKE[1]

THE common clypeastroids, *Echinarachnius* and *Mellita*, when adult, are characteristically of a brown or (in the former species) reddish-brown color. This seems to be general throughout the group. Taxonomic lists contain, however, numerous references to a greenish coloration of the test of these animals. When preserved in alcohol, or when dried, either after fixation in alcohol or after killing with fresh water, these sand dollars usually assume, for a time at least, a somewhat greenish color. Clark (1899, p. 118) says that specimens of *Mellita sesquiperforatus* Leske (=*sexforis* A. Ag.) collected at Jamaica were delicate olive green [when alive, I infer, though with doubt]. He also gives the coloration of specimens of this species obtained in Porto Rican waters as "usually light olive green (rarely brown) when alive." At Bermuda living individuals of this species are, he says, invariably brown, with no hint of green about them, either on the external surface or in the viscera. When killed in alcohol, however, they become green, and greenish pigment is dissolved by the fluid. This is also true of *Echinarachnius parma* (Clark, 1904, p. 564; Coe, 1912, p. 111).

Now, examination shows that there is at the bottom of this

[1] Contributions from the Bermuda Biological Station for Research, No. 90.

matter—in descriptive lists somewhat confusing—a rather interesting point, which it is the purpose of this note to elucidate.

Mellita, adult, is at Bermuda undoubtedly brown; large specimens (9.0–11.5 cm. in transverse diameter, usually 9.5 cm.), which I have from time to time collected by dredging upon grass-free bottoms of fine sand or mud at Flatt's Inlet, Spanish Point, Two Rock Passage, and other localities, are uniformly brown upon both aboral and oral surfaces, although the different individuals vary somewhat as to shade. Their general hue harmonizes well with that of the substratum. It is improbable that light has had a direct effect in producing pigmentation, since the oral surface, never turned toward the light, is at least as densely pigmented as the aboral one and is frequently (in larger specimens) darker. Young individuals in an active, healthy state were gotten in association with adults during the autumn months. Up to 5 cm. diameter, in one case 8 cm., they were found, with one exception in about 30, to exhibit no brownish coloration whatever; they were, on the contrary, *pure white,* and translucent, the yellowish stomach being easily made out through the test. These individuals were usually 3.5 to 4.0 cm. in transverse diameter. The one exceptional specimen, 2 cm. in diameter, was unusual because it was of a light coffee-brown shade.

When placed in alcohol, or in fresh water, these young *white Mellitas* became bright green; in sunlight the green on alcoholic specimens quickly disappears. Clark (1901, p. 254) notes that some young specimens of *M. pentapora* examined by him were green [in alcohol?].

When kept in aquaria for several days the small white "sea-plates" developed, in most cases, local indications of green pigment, although the animals were still quite active. This was also true of the large brown individuals. It was noticed that in cases where a large brown *Mellita* had been damaged by the cutting edge of the dredge, a green coloration was present along the wound when the haul was brought to the surface. Other specimens, apparently uninjured, sometimes developed an olive-green color on the oral surface within half an hour after being transferred from the dredge to a tub of sea water.

Thus the green coloration of *Mellita* is associated with a condition of injury or death. It is possible that the green material may have no connection with the substance responsible for the general brown integumentary coloration of adults.

The green pigment is readily extracted with fresh water. It is not chlorophyll. When an animal is allowed to die in fresh water, the integument and the ordinarily white internal parts of the skeleton of a *Mellita* become bright green. Putrefactive changes decolorize the green extract, and the color can not be restored by alkali, or with H_2O_2. Green extracts are also decomposed, irreversibly, by boiling.

The green color is not seen in faintly acid fresh-water extracts and the *Mellita* remains brown. If such an extract is made alkaline, the green color promptly appears in the extract. The substance responsible for the green hue in dead or injured parts of *Mellita* is in fact a very good indicator. It is colorless in acid, vivid green in alkaline solutions; this color change may be reversed many times. The "turning-point" of the indicator is at an acidity of $p_H = 7.6$–7.8—in a solution more alkaline than neutrality, but well on the acid side of the reaction of sea water ($p_H = 8.1 \pm$). This greening material seems to be present throughout the body of *Mellita,* as freshly secured bits of the (white) internal skeleton turn bright green in alkali. The few available references to the coloration of clypeastroids indicate that the alkali-greening substance regularly occurs in *Clypeaster* and in other genera of this group.

The ovaries of *M. sesquiperforatus* are heavily pigmented by a substance of the "antedonin"-"echinochrome" group. The mature egg itself is light brownish yellow, heavily yolked, and apparently larger than any echinoid egg that has been described. It measures about 0.26 mm. in diameter, and is thus about twice the size of the egg of *M. testudinata* (=*pentapora*), which measures 0.11 mm., though not so large as that of the brittle-star *Ophioderma,* 0.30 mm. in diameter (Grave, 1916, p. 439). The ovarian egg of *M. sesquiperforatus* is surrounded by a gelatinous envelope, the whole being 0.35 ± mm. in diameter. This envelope bears numerous evenly scattered clumps of precipitated reddish-purple pigment, the ovarian stroma being densely crowded with similar "chromatophores." In *Echinarachnius* the "chromatophores" of the egg-envelope are red rather than purple. The purple pigment of the *Mellita* ovaries exhibits the acid-alkali color changes and the absorption spectrum of the "echinochrome" pigments found in sea-urchins, holothurians, crinoids, and even in star-fishes; a dilute extract of a female *Mellita* may therefore be prepared which changes

from bright green to reddish purple at a hydrogen-ion concentration of about 7.5, the "echinochrome" not becoming orange until a much greater acidity is reached. This pigment becomes blue at an alkalinity of about $p_H = 8.2$; in the ovary it is reddish purple, but it is not in solution.

The interest of these facts lies not so much in their supplying some additional instances of the elaboration of similar (or even? identical) substances—conspicuously pigments—by animals related in descent, but in the evidence which is afforded regarding the reaction of intracellular fluids. Numerous cases illustrating the former point are available from among echinoderms, molluscs, tunicates, and so forth, and these cases have a certain importance for the general theory of animal coloration. But I am here chiefly concerned to point out that, if the alkali-greening substance present in *M. sesquiperforatus* is closely similar to that produced in the tissues of other clypeastroids, unequivocal statements as to the occurrence of greenish hues in living "sand dollars" may contain a suggestion as to a possible mode of origin for certain known geographical color differences in echinoderm species. I have not been able to find such references, but the point is worthy of further study. The evidence afforded by intracellular substances capable of behaving as indicators of acidity shows plainly that the tissues of marine animals are much more acid (less alkaline) than sea water. In *M. sesquiperforatus* the green color is produced when the tissue fluids become more alkaline than they customarily are; thus the integument, when injured or killed, becomes permeable to sea water and assumes a green hue. Healthy individuals for experimental work may, incidentally, be selected (at Bermuda) by the absence of green areas upon the test; the readiness with which greening is induced indicates the degree of care which must be employed in handling some marine animals. If by some means, for example, by higher temperature, the tissues of a *Mellita* population in a warmer sea were constantly maintained at a higher alkalinity than those at Bermuda, they might normally appear somewhat greenish in color. The normal variations in the coloration of *Chromodoris zebra,* a nudibranch containing an indicator favorable for such observations, strongly suggest that such differences in the reaction of intracellular fluids (not necessarily of the protoplasm) are entirely possible (Crozier, 1916). Whether or not comparable changes may be

induced as a regular thing in different oceanographic regions can not as yet be stated.

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PEMBROKE,
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A CASE OF ABNORMAL INHERITANCE IN DROSOPHILA MELANOGASTER

AMONG great numbers of cultures one is occasionally found which gives exceptional results not explainable by the usual mode of inheritance. Although such cases do not aid in understanding genetic problems unless the mechanism involved is worked out, the present case seems to be sufficiently remarkable to merit brief mention. The writer has no explanation to offer.

In culture 76, which was made up February 9, 1917, a large preponderance of males was observed, the ratio being 38 males to 3 females, and the males included unexpected classes. The parents of the culture were one homozygous eosin ruby forked female from stock and a male which was normal wild-type in all respects with the exception that the posterior cross veins of the wings were missing. His pedigree is unknown and he was

bred to determine whether the missing vein represented a genetic characteristic. This peculiarity probably had no relation to the exceptional nature of the offspring produced. The bottle was kept on the desk in the laboratory and the temperature was rather low most of the time, so that the larvæ developed slowly and the bottle became moldy before the flies finished hatching. It yielded exceedingly few flies, probably on this account as well as owing to the fact that nearly all the females were eliminated.

A count of the flies, as they hatched, gave 38 males and 3 females, a ratio which is inexplicable. The classes obtained were also as surprising. Owing to the cold the flies developed very slowly, so that the first offspring were removed on March 1 and comprised 18 eosin ruby forked sons. Four more hatched on the second and third, making a total of 22 eosin ruby forked sons which are of the expected class, since the three characteristics are sex-linked and the mother was homozygous for them. The count, continued until the thirteenth of March, gave a total of 3 normal females, which were expected in equal numbers with the males; 30 eosin ruby forked males; 2 eosin ruby males; 1 eosin male; 3 forked males; 2 normal or wild-type males.

The count in this case was kept up for more than the usual 10 days, but that could not have had any effect on the result in this case as no F_1 females were found until March ninth and could not have produced offspring, even had the temperature not been so low as to lengthen the incubation period beyond 13 days. The exceptional males, which are the cross-over classes ordinarily obtained in the F_2 generation from such a cross, could not be the result of a back-cross of the original mother to a son, as the only sons with which she could have come in contact were eosin ruby forked. In cases of primary non-disjunction, where sons inherit the sex-linked characters of the father, they inherit all his sex-linked characters, so that this can not be a case explainable by that means.

Contamination can hardly account for the results as the early males were of the expected class and later males always carried characters used in the cross, and the females were normal in appearance. Moreover, there is no known source of contamination that would give such a sex-ratio as this.

Results from the offspring were interesting but have not suggested any possible explanation of what occurred in the first generation. The eosin ruby forked sons were crossed out and

behaved quite normally in F_1 and F_2 generations. One forked son bred and gave offspring which behaved normally. The other two forked sons failed to produce any offspring, even though transferred to new bottles. The two eosin ruby sons were mated to bar females and afterwards rebottled with three females, but no offspring resulted. The eosin male also seemed to be sterile, as he was rebottled and remated without producing offspring.

The three daughters, which should have been heterozygous for eosin ruby and forked, and which have produced sons corresponding to that constitution, were crossed to brothers and gave the following unexpected results:

One in culture 88, mated to an eosin ruby forked brother, produced a total of 42 normal females, 74 forked females, 73 forked males, 37 normal males, and 13 eosin ruby forked males. A second in culture 93, mated to one of the wild-type brothers, produced 50 normal females and 28 forked females, 51 normal males and 73 forked males. The third daughter, mated to an eosin ruby forked brother, produced 2 normal, 35 forked, and 10 eosin ruby forked males; and 26 females all forked.

It is possible that the females were not virgin in these cases but that could not affect the sex-linked characters of the sons according to the normal mode of inheritance.

The two large classes of sons should have been the normal and eosin ruby forked classes, while the forked class of sons, which is the largest in all cases, should be no larger than the eosin ruby class, which does not occur even once.

Efforts to determine what was causing this abnormal inheritance were unsuccessful, because further breeding experiments showed the offspring of all classes to behave quite normally in all respects.

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